

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3402, 32 pp., 21 figures, 1 table March 27, 2003

Osteology and Relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae)

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ABSTRACT

The troodontid *Byronosaurus jaffei* is known from two specimens from adjacent localities in the Nemegt basin, Ömnögovi Aimag, Mongolia. These specimens are composed of well-preserved cranial material and fragmentary postcrania. All of these elements are described here. *Byronosaurus jaffei* is included in a comprehensive phylogenetic analysis of Coelurosauria to ascertain its relationships. Several interesting characters of *Byronosaurus jaffei* have implications both for theropod relationships and for understanding patterns of variation within coelurosaurian theropods. These include the position of a foramen that marks the exit of the supra-alveolar canal (which we suggest is homologous with the subnarial foramen), the flattened internarial bar, the unusual interfenestral bar, and the unserrated teeth. Additionally, the well-preserved braincase allows detailed comparison with other troodontid taxa.

INTRODUCTION

The remains of troodontid dinosaurs are extremely rare, and only nine taxa have been

described, most from Central Asia (Osmólska and Barsbold, 1990; Russell and Dong, 1993). Here we provide a detailed description of *Byronosaurus jaffei*, a troodontid

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Fig. 1. The holotype locality looking north. The arrow signifies the point of discovery of IGM 100/983.

from the Djadokhta Formation at Ukhaa Tolgod that was named and briefly described by Norell et al. (2000). Only one other troodontid, *Saurornithoides mongoliensis* (Osborn, 1924), has been reported from Djadokhta, or Djadokhta-type, beds in Asia (Currie and Dong, 2001a). Although troodontids are rare, well-preserved braincases are known for several taxa (Osborn, 1924; Barsbold, 1974; Currie, 1985; Currie and Zhao, 1993; Russell and Dong, 1993; Xu et al., 2002), and have provided important phylogenetic insights into this clade.

Few phylogenetic studies within Troodontidae have been undertaken, and broader studies that include troodontids and their purported closest relatives (dromaeosaurids [Gauthier, 1986; Sereno, 1999], birds [Holtz, 2001]) have not taken into account the variation among troodontid taxa and have been hindered by fragmentary material and inadequate descriptions. Here we expand our species-level phylogenetic analysis of the group (Norell et al., 2000) and examine the evidence for monophyly of this group and more exclusive clades within it. The evidence for the relationships of troodontids to other

groups will be considered in more detail elsewhere.

MATERIAL

LOCALITY: The holotype specimen (IGM 100/983) was discovered at the sublocality called “Ankylosaur Flats” in 1993 by Michael Novacek (fig. 1). Additional remains of this specimen were collected during the 1994 and 1995 field seasons. Unlike many of the fossils at Ukhaa Tolgod, the specimen was not articulated and was found as a loose association of bones. Nevertheless, the rostral fragment and the braincase were found in place adjacent to one another in life position, separated by a zone of weathering. The remaining parts of the skeleton were collected as eroded pieces below the skull. Later examination of the specimen revealed that remains of a second individual were intermixed with IGM 100/983. This individual (IGM 100/987) is significantly larger than IGM 100/983, and consequently its bones can easily be separated. This specimen lacks troodontid apomorphies, and is referred to

the Ornithomimidae (Makovicky and Norell, 1998).

REFERRED SPECIMEN: A second specimen (IGM 100/984) was collected on July 15, 1996 at the "Bolor's Hill" locality approximately 6 km west of the main Ukhaa Tolgod exposure. While extremely fragmentary, the specimen preserves some important features not present on the type. The specimen consists of a rostrum in six pieces. It is referred to *Byronosaurus jaffei* on the basis of supernumary teeth all lacking serrations, distinctive lacrimals with a lateral shelf that overhangs the anterodorsal corner of the orbit, and a pair of passages through the interfenestral bar, which is not recessed from the plane of the rostrum.

DIAGNOSIS

Byronosaurus jaffei exhibits the following troodontid synapomorphies (Xu et al., 2002): numerous teeth, close packing of dentary dentition near the rostral tip of the lower jaw, presence of a distinct groove for the neurovascular foramina on the dentary, and a dorsoventrally flattened internarial bar.

Byronosaurus jaffei is part of a clade comprising all troodontids except the basal taxon *Sinovenator changi*. This clade is ambiguously diagnosed by: braincase displaying a large pneumatic sinus (the "lateral depression" ventral and anteroventral to the braincase; presence of a subotic recess; extensive anterior process of the lacrimal forming the dorsal border of the antorbital fenestra; and maxillary participation in the posterior margin of the nares. Ambiguity in the optimization of these characters is due to missing data and multiple placements of several troodontid taxa, including *Byronosaurus jaffei*, *Sinornithoides youngi*, and an unnamed Mongolian taxon represented by IGM 100/44.

Byronosaurus jaffei can be distinguished from all other troodontids by the possession of several derived characters, including teeth lacking serrations, an interfenestral bar that is not recessed from the plane of the maxilla, and a shallow groove along the buccal margin of the maxilla.

DESCRIPTION

The skull of IGM 100/983 is preserved in two parts. The anterior section comprises the rostrum and articulated dentaries that have been transversely compressed although most bones appear uncrushed (figs. 2, 3). It was found in two pieces that have been glued together, and the glue fills some large gaps along the contact. The anterior section ends at the anterior margin of the orbits. The braincase was preserved separately and has not been crushed. The top of the braincase is missing, exposing an eroded endocast, and some delicate outer parts of the basicranium are incomplete.

IGM 100/984 is very fragmentary. It was preserved as eight separate nodules, only three of which contain recognizable elements. One contains the premaxillae and the anterior ends of the maxillae (fig. 4), a second contains a section of the rostrum at the level of the interfenestral bar, and a third contains a section of skull roof at the preorbital bar preserving the lacrimals and the posterior part of the nasals.

Our description is primarily based on IGM 100/983, supplemented by IGM 100/984. Measurements of the holotype IGM 100/983 are tabulated in appendix 2. Comparisons with *Saurornithoides junior* are based on Barsbold (1974, 1983) and are supplemented by our own observations. Comparisons with *Troodon formosus* are based on Currie (1985) and Currie and Zhao (1993), and those with *Sinornithoides youngi* are based on Russell and Dong (1993) and our examination of the specimen. Comparisons with *Saurornithoides mongoliensis* are based on our own observations of the type (AMNH 6174). Other comparisons are referenced herein.

The face and braincase of the type specimen (IGM 100/983) were scanned separately in May 1997 at The University of Texas High-resolution X-ray Computed Tomography Facility. Both were scanned on the high-resolution subsystem, based on a Feinfocus microfocal X-ray tube and an image-intensifier detector system. The face was scanned with X-ray energy set at 120 kV, 0.200 mA, at 190% offset in an air wedge, with a source-object distance of 85 mm. Slice thickness is 0.25 mm, and 562 consecutive slices

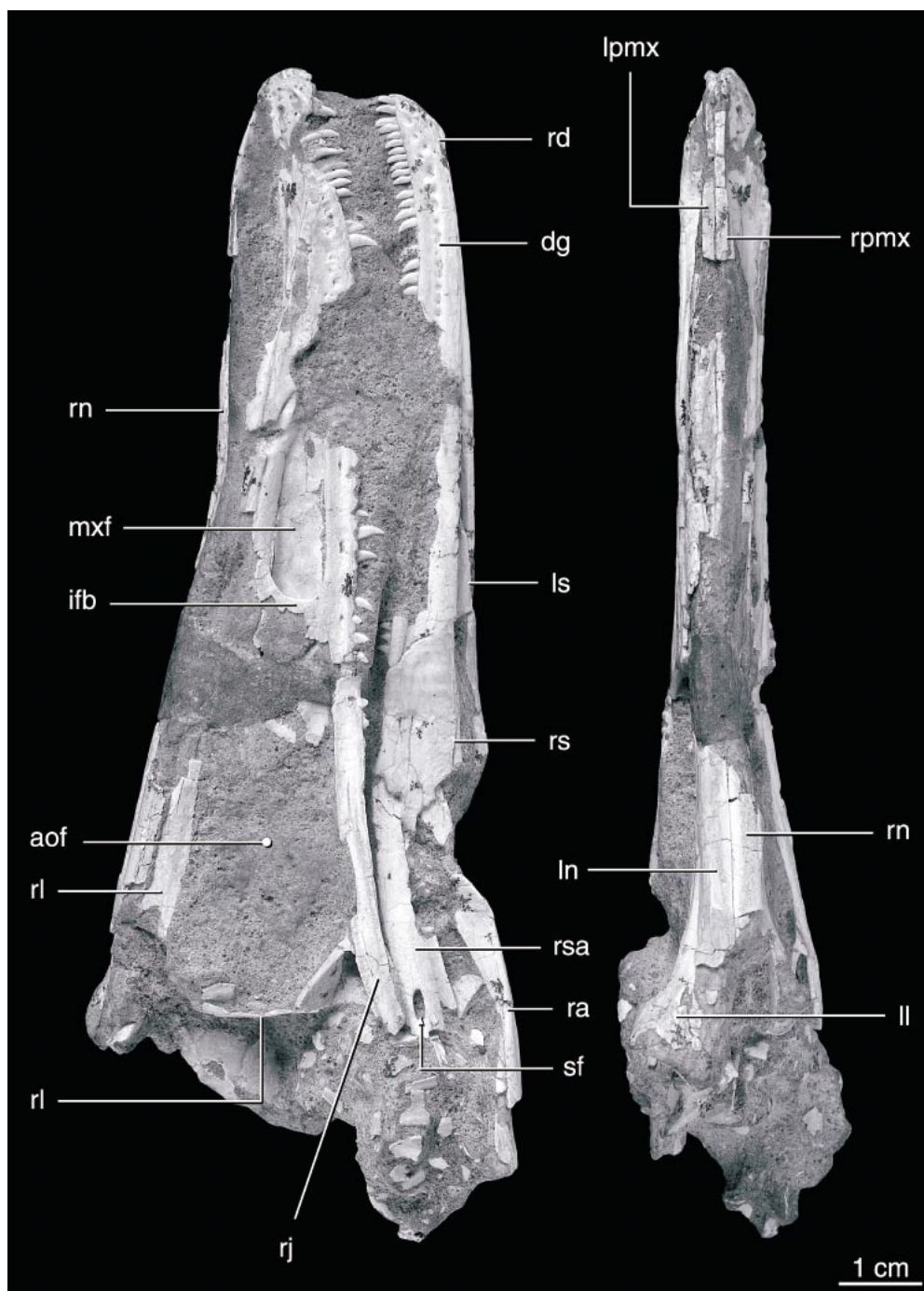


Fig. 2. The rostrum of the holotype specimen IGM 100/983 in right lateral and dorsal views. Abbreviations are listed in appendix 1.

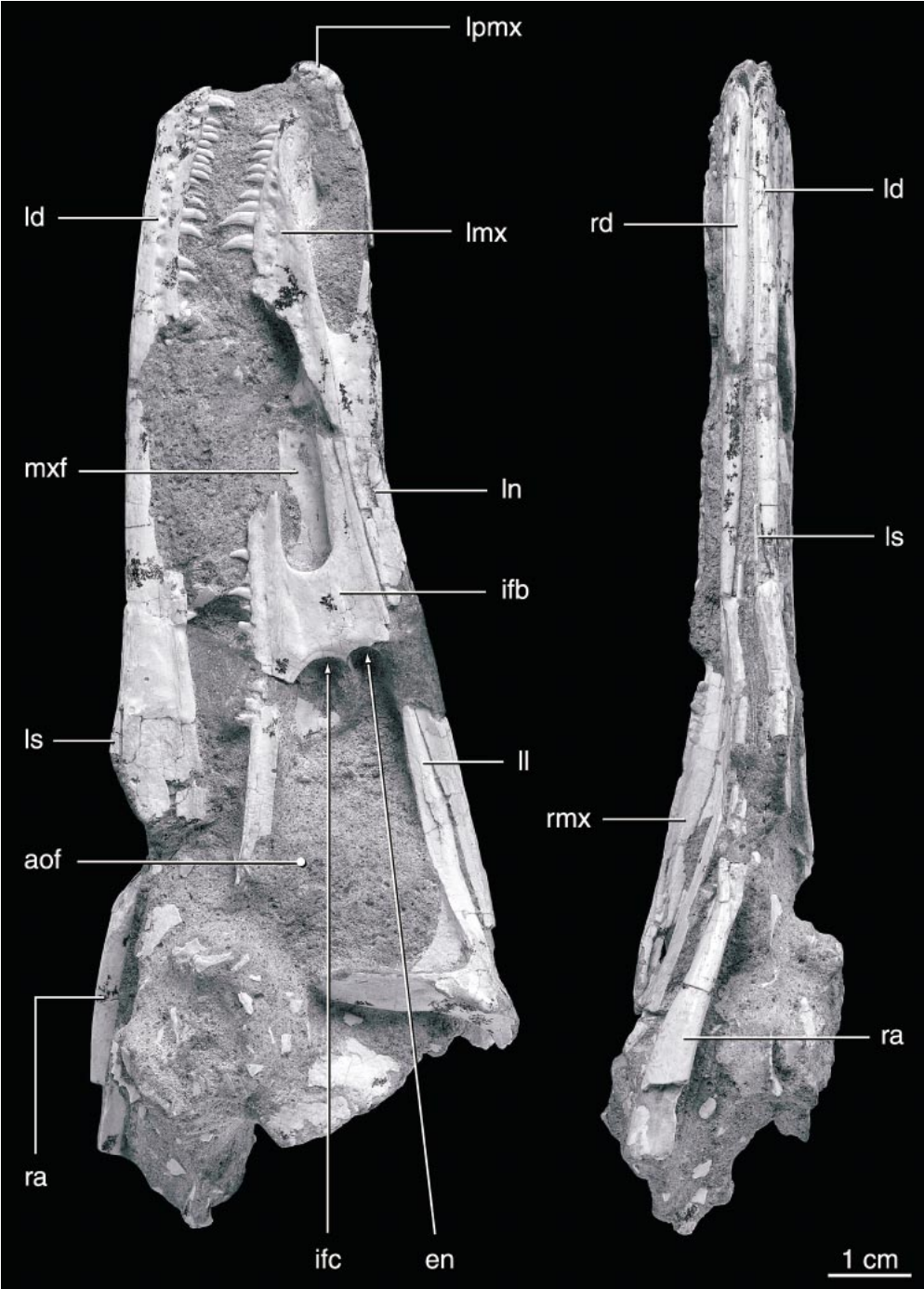


Fig. 3. The rostrum of the holotype specimen IGM 100/983 in left lateral and ventral view. Abbreviations are listed in appendix 1.

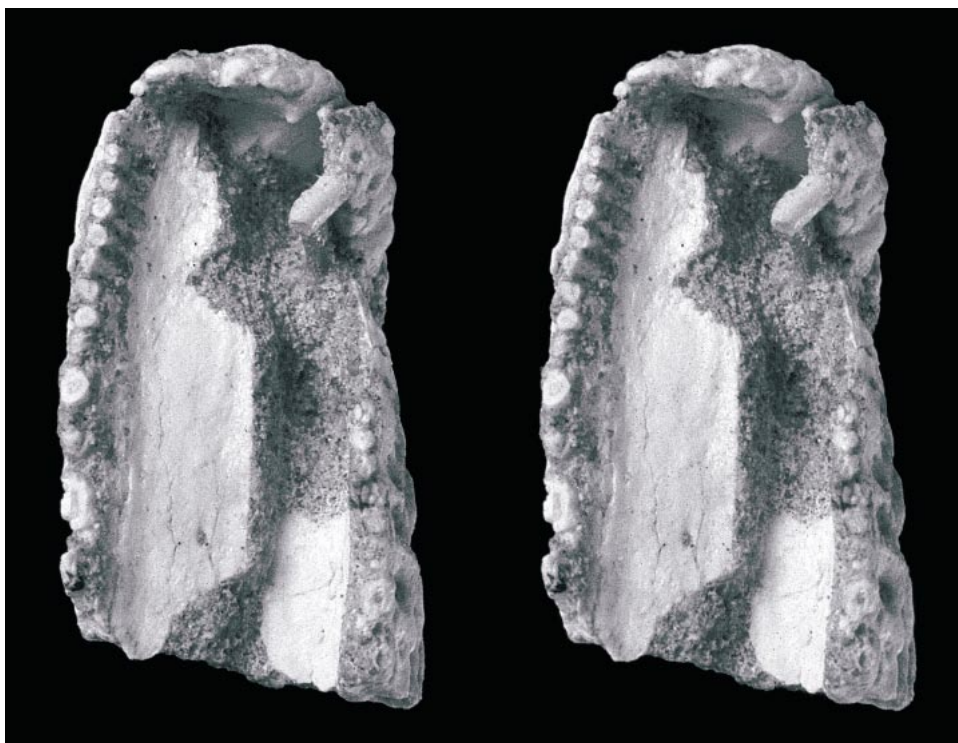


Fig. 4. Stereopair of the ventral surface of the premaxillary area in the referred specimen IGM 100/984.

were generated. For each slice, 1200 views were taken with two samples per view. Reconstructed 512×512 pixel imagery was exported as 8-bit TIF files. The braincase was scanned with X-ray energy set at 120 kV, 0.400 mA, at 190% offset in an air wedge, with a source-object distance of 45 mm. Slice thickness is 0.20 mm, and 150 consecutive slices were generated. For each slice, 1200 views were taken with two samples per view, and a field of view of approximately 36.3 mm. Reconstructed 1024×1024 pixel imagery was exported as 8 bit TIF files. Original CT datasets were archived on CD-ROM at the University of Texas and the American Museum of Natural History. Animated serial section movies and three dimensional volumetric reconstructions are also viewable on the Internet at www.DigiMorph.org.

THE ROSTRUM

PREMAXILLA: Paired premaxillae form the anterior margin of the skull. Each premaxilla

bears four teeth (fig. 4), as is primitive for theropods. The nasal process is gently arched and dorsally flattened and triangular in cross section (fig. 2), and it forms the anterodorsal margin of the external narial opening. It is thin anteriorly and increases in breadth in the area where it divides the nasals along the midline, as in *Saurornithoides junior*. The maxillary process is short and heavily pitted by small foramina on its small facial surface. Medially, the surface of the maxillary process arches to form the floor of the naris (fig. 2). There is no posterior process as in dromaeosaurids that excludes the maxilla from participation in the margin of the narial opening (figs. 2, 3). Although obscured, the suture with the maxilla is apparently very simple.

MAXILLA: The maxilla forms most of the lateral surface of the skull. Anteriorly, it forms much of the floor of the large naris. The maxilla contacts the premaxilla along a straight suture anteriorly in this chamber (figs. 4, 5). Just posterior to this suture, and before the maxilla rises from the narial floor

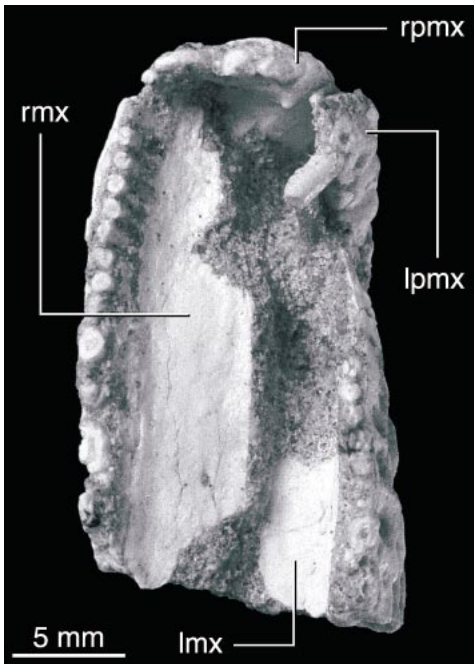


Fig. 4. Continued.

to form the posterodorsal margin of the naris, lies a large, anteriorly directed foramen that is completely enclosed by the maxilla (figs. 5, 6). A similar foramen is observed in the alvarezsaurid *Shuvuuia deserti* (IGM 100/977). This foramen enters into a long supra-alveolar canal that parallels the tooth row (fig. 6). The maxilla rises from the narial floor in a gentle posterior slope. The lateral surface below the narial chamber is covered with small pits and foramina (fig. 5). These are most apparent as a row of large pits that lie in a groove just dorsal and parallel to the dentigerous margin. This row of pits runs posteriorly below the maxillary fenestra, decreasing in density posteriorly until they disappear below the antorbital fenestra.

The lateral surface of the maxilla is perforated by two large, elongated antorbital openings (figs. 2, 3). The maxillary fenestra is elliptical and extends from below the external nares to the midway point between the maxillary-premaxillary suture and the pre-orbital bar. This fenestra has an osseous medial wall, which is perforated by a small hole in slightly different positions on each side, but these holes may be weathering artifacts.

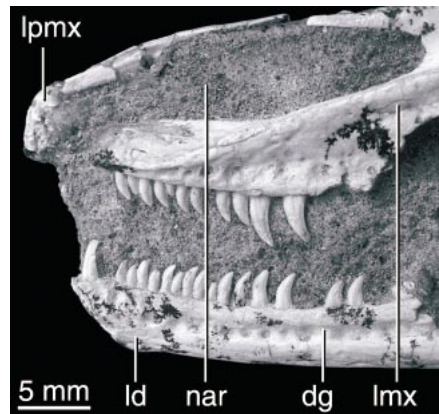


Fig. 5. Detail of the narial region of the holotype specimen IGM 100/983 in left lateral view. Abbreviations are listed in appendix 1.

In *Troodon formosus* the maxillary fenestra is backed by an unperforated osseous wall. (Brochu, personal commun.). Anteriorly, the rostral end of the maxilla overhangs the maxillary fenestra to form a large pocket. The maxillary fenestra is separated from the antorbital fenestra by a large, very flat plate of maxilla, here termed the interfenestral bar (figs. 2, 7). Unlike *Saurornithoides junior*, *Saurornithoides mongoliensis*, or *Sinornithoides youngi* (Currie and Dong, 2001a), the interfenestral bar is not inset from the plane of the maxilla.

The main antorbital fenestra lacks an osseous floor, is larger than the anterior fenestra, is subtrapezoidal in shape, and narrows dorsally. Anteriorly, the margin of the fenestra is formed by the interfenestral bar, which is scalloped in two places (fig. 7). These emarginations lead to dorsal and ventral passages through the interfenestral bar, which are separated by an osseous wall (fig. 7). An erosional cross section of the snout of IGM 100/984 exposes the course of the two channels through the interfenestral bar (fig. 8). The dorsal emargination marks the caudal end of the narial passage, which is visible laterally as a swollen ridge on the dorsal part of the osseous wall of the maxillary fenestra (figs. 9, 10). The ventral canal connects the antorbital and maxillary fenestrae. The caudal entrance into the supra-alveolar canal, which transmits the innervation and blood supply of the maxillary dentition, lies on the

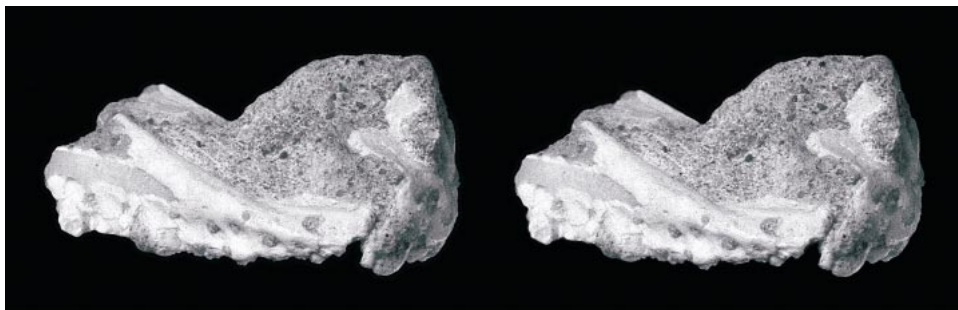


Fig. 6. Stereopair of the right dorso-oblique dorsal surface of the rostrum in the referred specimen IGM 100/984. Notice the entrance to the supra-alveolar canal (fsac) which we interpret as the subnarial foramen. Abbreviations are listed in appendix 1.

medial face of the interfenestral bar (fig. 9C). Below the antorbital fenestra, the maxilla is extremely thin, dorsoventrally concave, and devoid of the small foramina that are so conspicuous anteriorly.

On the palate of IGM 100/984, longitudinally extensive palatal shelves of the maxilla form the roof of the mouth (figs. 4, 9, 10). These large palatal flanges extend posteriorly from the contact with the premaxilla, and are joined by a median vomer at the border of the choanae (figs. 11, 12). Together these form a solid secondary palate on the roof of the mouth extending to the choanae, which lie between the antorbital fenestrae.

NASAL: The nasal is a long bone that covers the top of the rostrum for most of its length (fig. 2). Anteriorly, the nasal forms the posterolateral boundary of the large external naris. The nasal is wider anteriorly than posteriorly. As preserved, anteriorly the nasal is laterally convex, forming a continuous transition from a vertical plane anteriorly to a horizontal plane posteriorly. This transition is marked by a sharp angle, but the angle may be influenced by postmortem distortion. A maxillary process extends posteroventrally, while a long, attenuate premaxillary process extends anteriorly to form the posterodorsal border of the naris for half its length and contact the nasal process of the premaxilla medially (fig. 5). This process gives the anterior surface of each nasal a concave appearance in lateral view. The lateral edge of the nasal contacts the maxilla anteriorly and the lacrimal posteriorly along a straight suture. Parallel and just medial to this suture lies a row

of tiny foramina within a shallow depression. The posterior contact with the frontal is not preserved on the type specimen, but is visible on IGM 100/984. The nasals end just posterior to the level of the preorbital bar. At the level of the preorbital bar the nasals diverge along the midline (fig. 13) to accommodate a missing anterior wedge of the frontal, as in *Saurornithoides junior*. Posterior to the preorbital bar on the top of the skull the nasals are flat, and together with the lacrimals they form a flat surface above the anterior part of the orbits (fig. 13).

LACRIMAL: The lacrimal forms the anterior and anterodorsal border of the orbit. In lateral view the lacrimal is T-shaped, as in dromaeosaurids; however, the anterior or supra-orbital fenestral process is much longer than the supraorbital process (figs. 2, 3). Although poorly preserved, several important features are apparent. The preorbital bar is a straplike process extending from the skull roof to contact the jugal. The preorbital bar is oriented nearly vertically; however, this orientation may be influenced by distortion. Contact with the jugal is preserved only on the right side, where a posterolaterally opening foramen appears to be present, but this area is broken (fig. 2). The posterior surface is slightly convex in cross section. CT scans reveal that the lacrimal duct exits the orbit just ventral to the contact between the anterior and posterior processes. Currie and Dong (2001a) suggested that a lacrimal duct is absent in troodontids, but in *Byronosaurus* the lacrimal duct passes through the lacrimal and opens into the posterodorsal corner of the

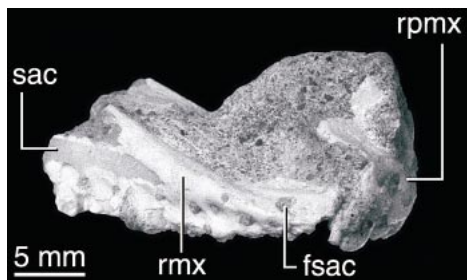


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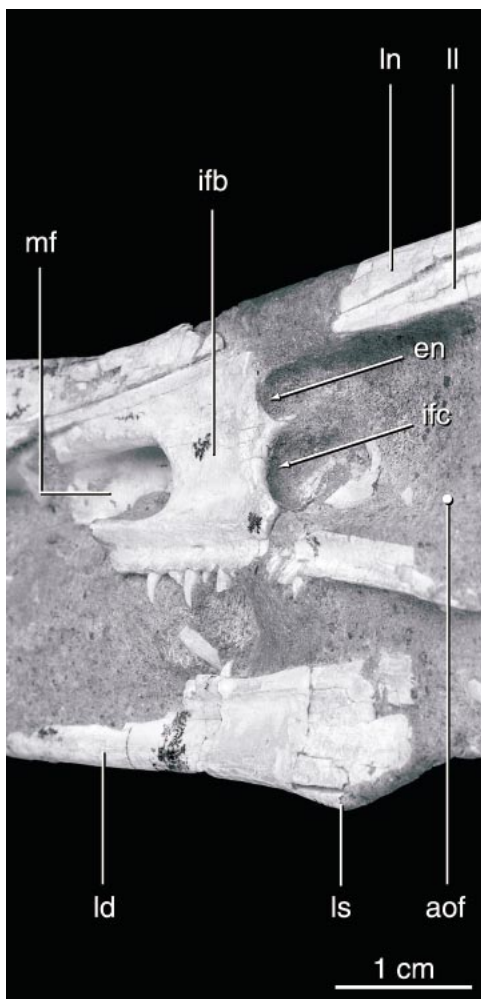


Fig. 7. Postero-oblique view of the left side of the rostrum of IGM 100/983 showing the two passages through the interfenestral bar. The upper passage (en) connects with the nasal chamber. The lower passage (iac) connects with the maxillary sinus.

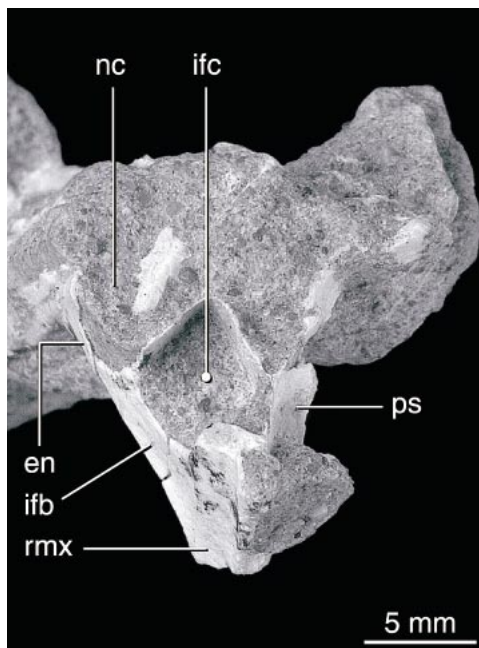


Fig. 8. Antero-ventro oblique view of the referred specimen (IGM 100/984) showing the osseous wall of the interantorbital canal (iac) separating it from the nasal chamber just anterior to the interfenestral bar. Abbreviations are listed in appendix 1.

antorbital fossa, as observed in IGM 100/984. The posterior, or supraorbital, process is preserved only at its base on the type. On IGM 100/984 the posterior process is apparently completely preserved on the right lacrimal (fig. 13). In this specimen it extends to the same level posteriorly as the nasals. The posterior process forms a laterally expanded shelf above the orbit, as in *Saurornithoides junior*, and it apparently meets the frontal along a posteromedial-anterolateral diagonal suture (fig. 13). Just posterior to the level of the preorbital bar, the dorsal surface of the lacrimal is perforated by a small anteriorly directed foramen.

The anterior process is extensive and forms most, if not all, of the dorsal border of the posterior antorbital fenestra. At the posterodorsal corner of the antorbital fenestra a large pocket is formed by a buttress between the preorbital and anterior processes of the lacrimal. The lateral surface of this buttress is extensive and flat, forming a wall to the

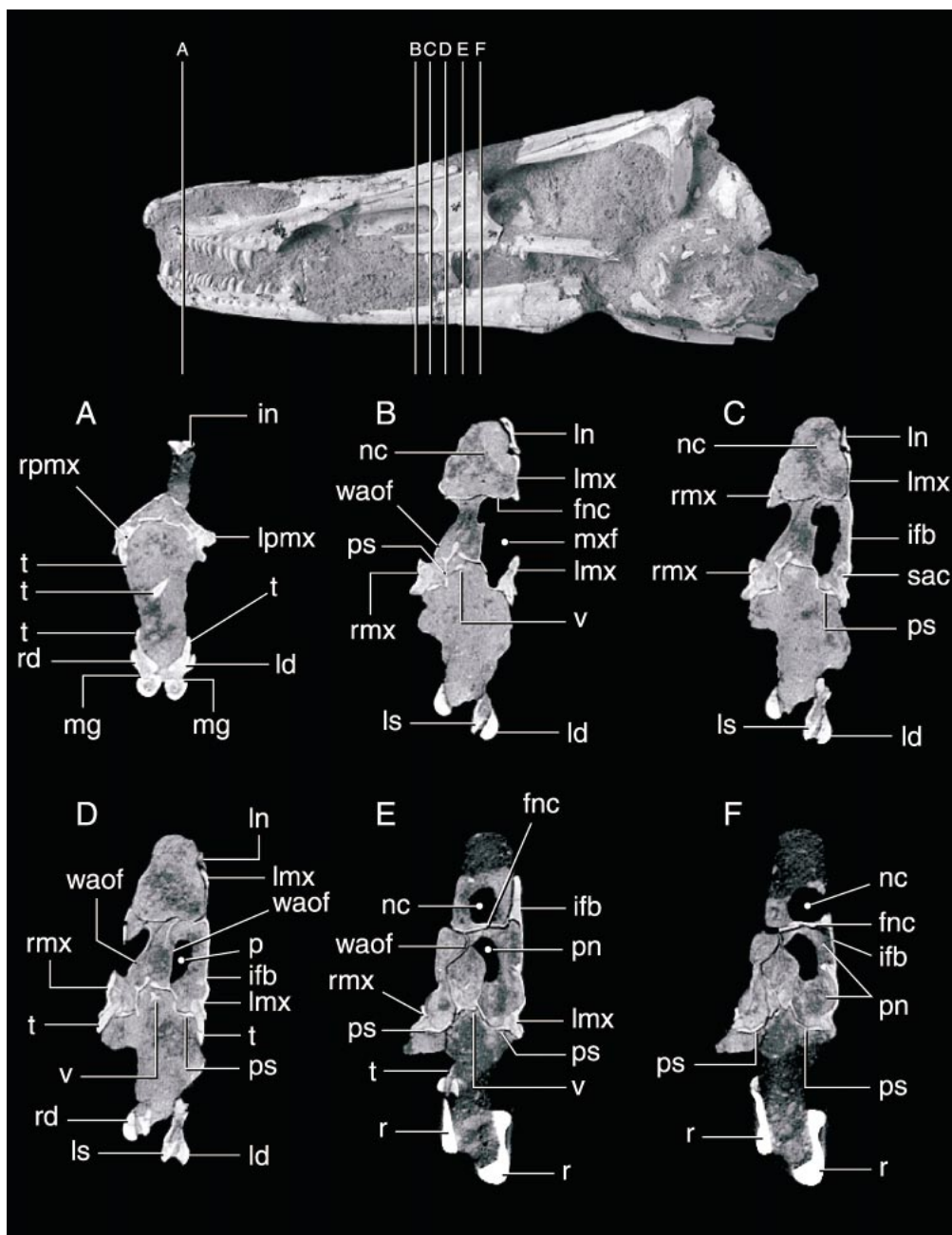


Fig. 9. CT scans of the rostrum of IGM 100/983. Notice the osseous floor to the nasal cavity (fnc) as it extends through the interfenestral bar in C, D, E, and F. Abbreviations are listed in appendix 1.

posterodorsal part of the antorbital fossa. A small ridge on the anterior process overhangs the pocket. The pocket that forms at the apex of the buttress is smooth-walled and is pierced at its apex by the lacrimal duct.

JUGAL: The jugal is extremely poorly represented by only a small strap of bone from the anterior end, present on the right side of IGM 100/983 (fig. 2). The preserved fragment of the jugal is a very thin bone that

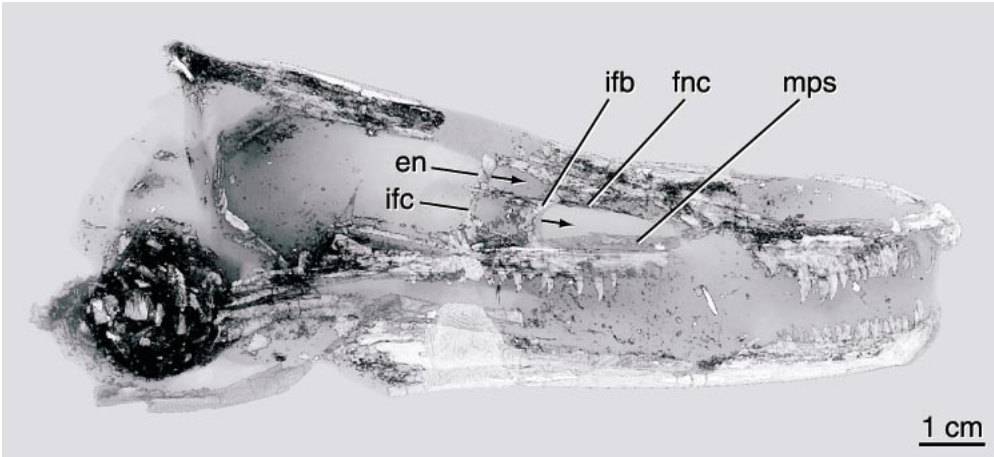


Fig. 10. Rendered view of the holotype rostrum of IGM 100/983 showing the narial chamber in relation to the maxillary sinus and the palate. Abbreviations are listed in appendix 1.

contacts the jugal process of the maxilla along an overlapping suture where the jugal is exposed on top of and lateral to the underlying maxilla. The element is dorsoventrally concave laterally. Only a short section of the suborbital process is preserved on the right side.

PALATINES: Only the anterior interchoanal bar of each palatine is preserved. Although these flat bars are displaced and almost hor-

izontal in the holotype skull, they would probably have met dorsally to form a narrow trough above the choanae, as in *Velociraptor mongoliensis* (Barsbold and Osmólska, 1999). The anterior tips of the palatines may have reached the caudal end of the median chamber beneath the nasal passage, although there is a lot of breakage in the parts near the interfenestral bar.

VOMER: The base of the paired posterior

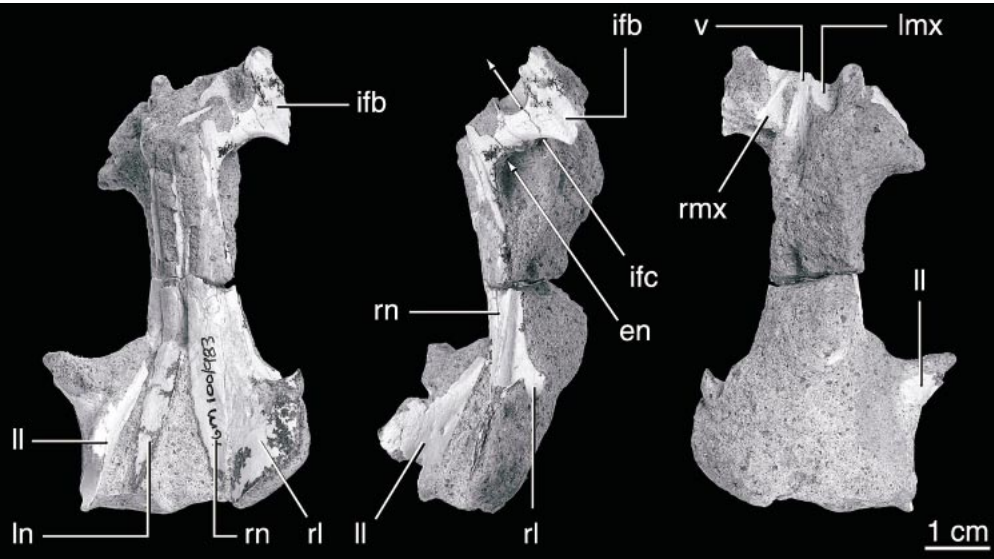


Fig. 11. Section of the rostrum in IGM 100/984 in dorsal, right lateral, and ventral views. Abbreviations are listed in appendix 1.

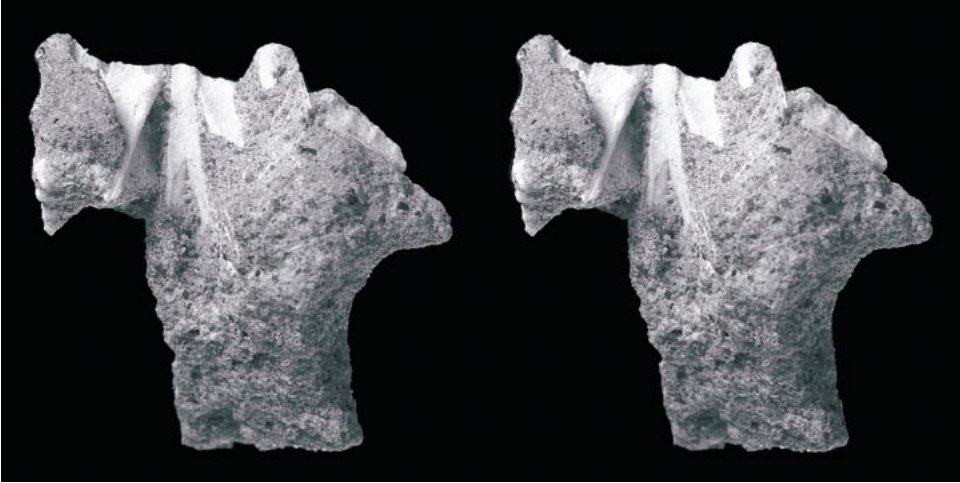


Fig. 12. Stereopair of the palatal region of IGM 100/984 in ventral view. Abbreviations are listed in appendix 1.

section of the vomer is preserved between the caudal ends of the maxillary palatal shelves in IGM 100/984 (fig. 11). At the level of the interfenestral bar, the posterior processes conjoin to form a single median element (fig. 10B, D). In the serial CT sections of the holotype skull, the vomer appears to end posterior to the external naris, unlike the condition in *Velociraptor mongoliensis* (IGM 100/986).

PNEUMATIC SYSTEMS OF THE SNOUT

The snout comprises a complex of three longitudinal passageways that pass from just

behind the nares back toward the choanae. On either side of the snout, the accessory antorbital fenestra connects to the antorbital fenestra through the lower, pneumatic passage through the interfenestral bar (figs. 8, 10). A blind, median chamber termed the maxillary antrum by Witmer (1997a) intercedes between these paired pneumatic systems (fig. 9C–F). It extends from below the caudal end of the naris to the interfenestral bar and is roofed by the nasal passage and floored by the palate. Its lateral walls are formed by the vertical laminae of the maxilla that form the wall of each maxillary fenestra



Fig. 13. Stereopair of the lacrimal-nasal area of IGM 100/984 in dorsal view. Notice the large extensions of the lacrimal over the antorbital bar. Abbreviations are listed in appendix 1.

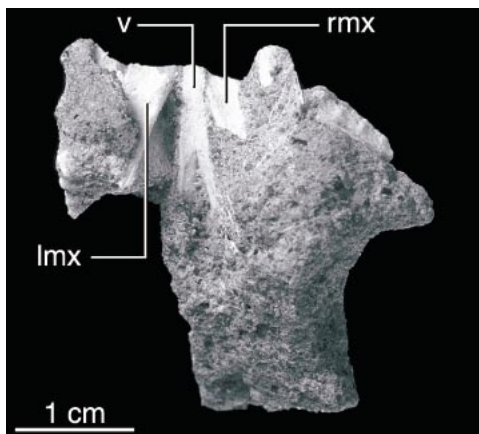


Fig. 12. Continued.

(waof in figs. 2, 3, 9B-F). The chamber opens caudally between the interfenestral bars and just anterior to the level of the caudal end of the nasal passage. The palatines contribute to the ventromedial floors of the lateral passageways, and possibly to the floor of the median passage.

THE BRAINCASE

The braincase was collected in a single weathered nodule (figs. 14, 15). Although several of the elements have been lost to erosion, many important features are well preserved and allow additional insight into cranial anatomy and its variation in troodontid dinosaurs. The front and top of the braincase are missing, as is the occipital condyle and the right paroccipital process. Sutures among

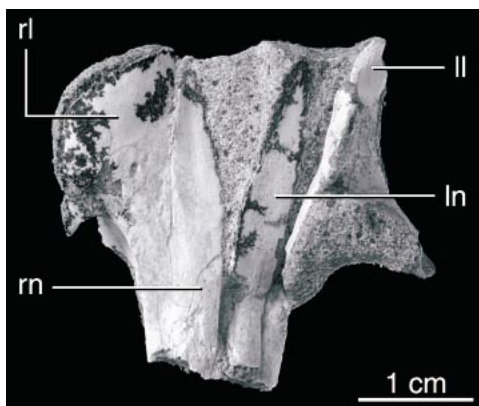


Fig. 13. Continued.

braincase elements are not apparent, indicating that the animal was an adult. Consequently, this description relates to morphological features rather than specific cranial elements.

OCCIPITAL SURFACE: The occipital surface is heavily weathered and the occipital condyle is missing (fig. 14). The short paroccipital process is oriented nearly parallel to the plane formed by the medial part of the occiput surrounding the foramen magnum (figs. 14, 15). Although the opisthotic may have contributed to the paroccipital process (Currie, 1985), no suture to distinguish this is apparent. The paroccipital process is divided into medial and lateral parts by a low ridge that runs ventrolaterally from the top of the occiput. At the ventral surface of the diagonal ridge is a small pit that may represent the foramen for the occipital artery. Ventral to the paroccipital process, the margin of the occipital surface is formed by the metotic strut, which is separated from the paroccipital process by a small notch (fig. 14).

Ventrolateral to the ventral limit of the foramen magnum are three foramina (fig. 14). A large dorsomedial and a smaller ventromedial foramen transmitted branches of the hypoglossal nerve (CN XII) through the braincase wall. A large, more ventrolateral foramen vagi is hidden in posterior view by a scalloped shelf that is a continuation of the ventral border of the paroccipital shelf onto the occiput. It presumably transmitted the vagus (CN X) and spinal accessory (XI) nerves from the metotic foramen through the occiput. Just ventral to this cluster of foramina near the presumed location of the exoccipital-basioccipital suture lies a small rugose bump.

A pair of small basioccipital tubera lie directly ventral to the foramen magnum (figs. 14, 15). They lack distinct subcondylar foramina opening into the anterior pneumatic spaces, although they are pneumatized laterally by the subotic recesses. The tubera are separated by a medial wedge-shaped depression at the apex of which is a small pit that apparently does not lead to a foramen.

LATERAL WALL OF THE BRAINCASE

Like other troodontids the lateral surface of the braincase is marked by a large lateral

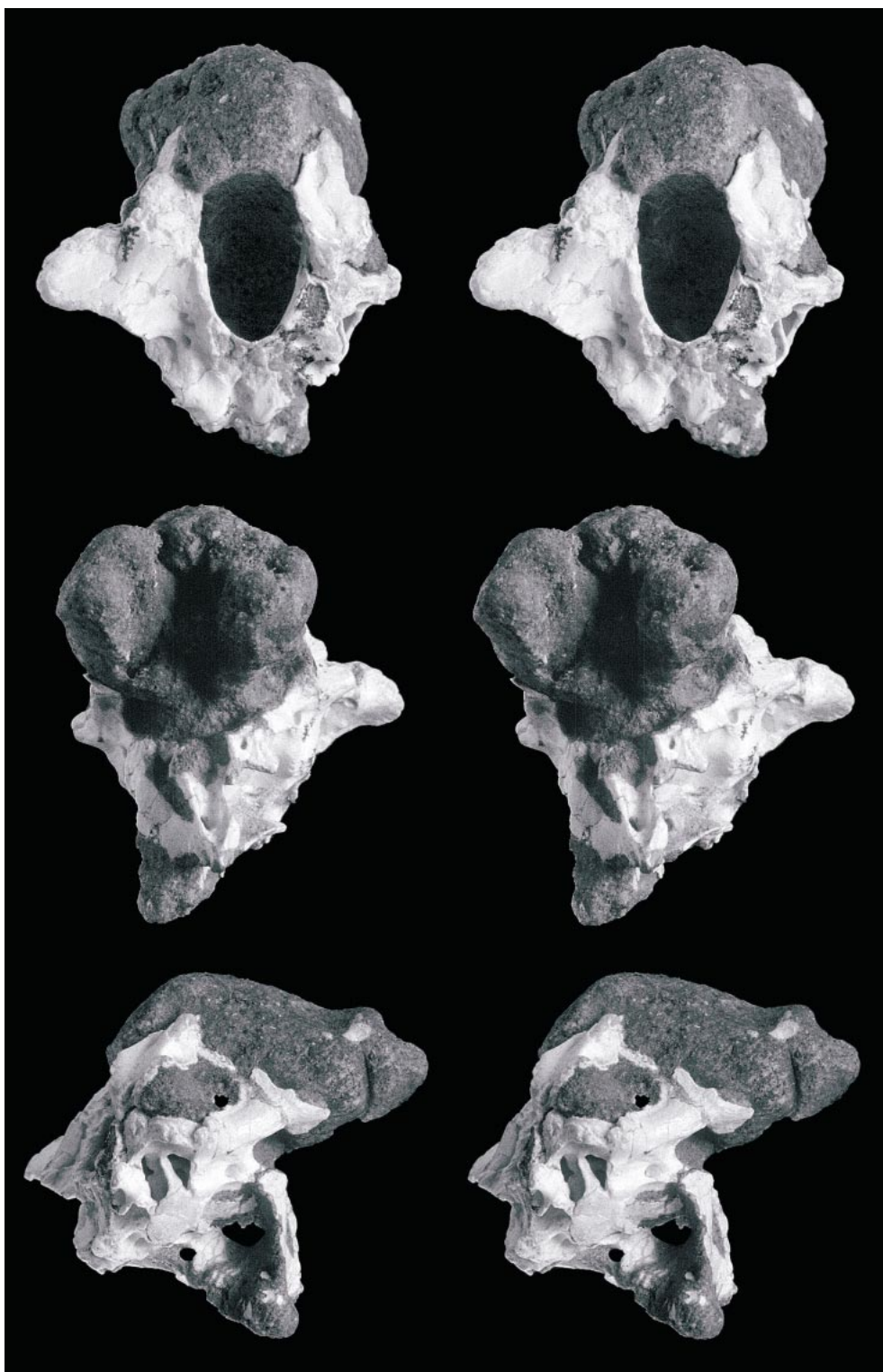


Fig. 14. Stereopairs of the braincase of the holotype specimen IGM 100/983. Top, posterior; middle, anterior; lower, right lateral views. Abbreviations are listed in appendix 1.

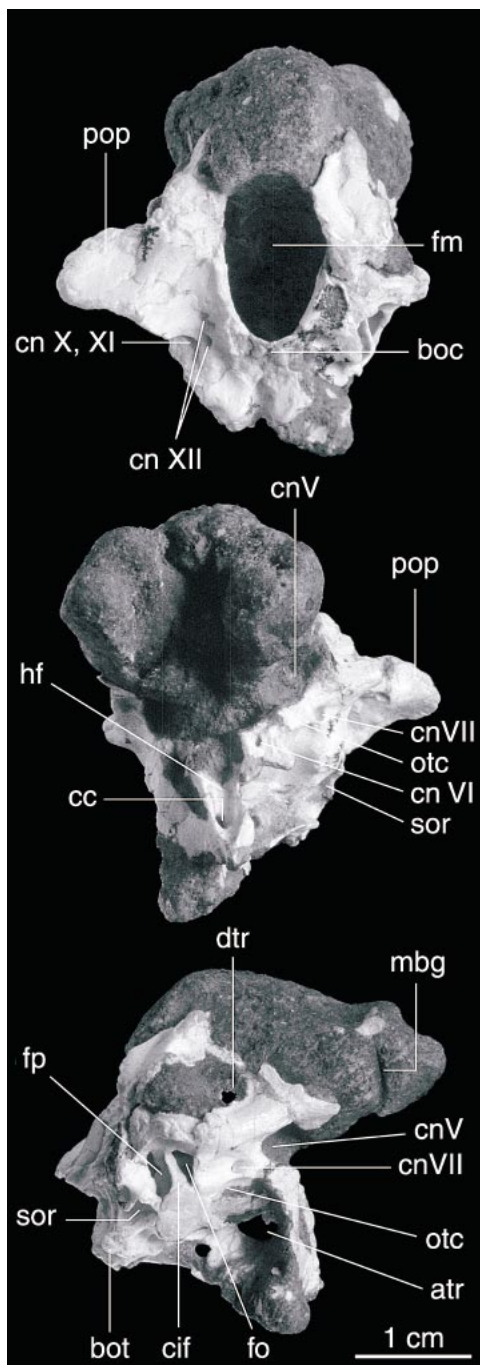


Fig. 14. Continued.

depression bounded by an otosphenoidal crest anteroventral to the middle ear (figs. 14, 15).

LATERAL DEPRESSION AND SIDE WALL OF THE BRAINCASE: A sharp otosphenoidal crest originates just ventral to the foramen for the facial nerve (CN VII) and curves anteroventrally, bounding the lateral depression anteriorly and dorsally (fig. 15). The lateral depression is bordered posteriorly by a subotic recess that lies ventral to the metotic strut and invades the basal tuber. Although prominent, the lateral depression is not as deep as in *Troodon formosus* (Currie and Zhao, 1993) and *Saurornithoides junior* (Barsbold, 1974).

Ventrally, the left and right lateral depressions appear to be separated only by a thin lamina that extends posterior to the hypophyseal fossa. Although poor preservation makes it difficult to determine the extent of this lamina, connections between the left and right lateral depression may have been present, as in *Troodon formosus* (Currie and Zhao, 1993).

The wall of the braincase surrounding the hypophyseal fossa defines the anteromedial corner of each lateral depression (figs. 14, 15). Each internal carotid passage descends anteroventrally through an osseous canal and meets its counterpart immediately before entering the hypophyseal fossa itself in a common carotid opening (fig. 14).

The middle ear is proportionately large in this taxon. An osseous crista interfenestralis subdivides the middle ear into a smaller, triangular anterior aperture (the fenestra ovalis) and a larger fenestra pseudorotunda posteriorly (figs. 14, 15). The crista interfenestralis is thinner dorsally than ventrally, and a suture at the base of the interfenestral crest suggests that it is formed entirely from the bone that forms the dorsal rim of the middle ear cavity (the opisthotic in *Troodon*, according to Currie and Zhao, 1993). Anteromedial to the interfenestral crest, the inner ear forms a deep cochlear recess that is partly divided into wider proximal and more constricted distal parts by a low ridge extending obliquely along the medial wall. A foramen located in the anterior chamber of the cochlear recess opens anteromedially into the braincase below the vestibular pyramid, and probably

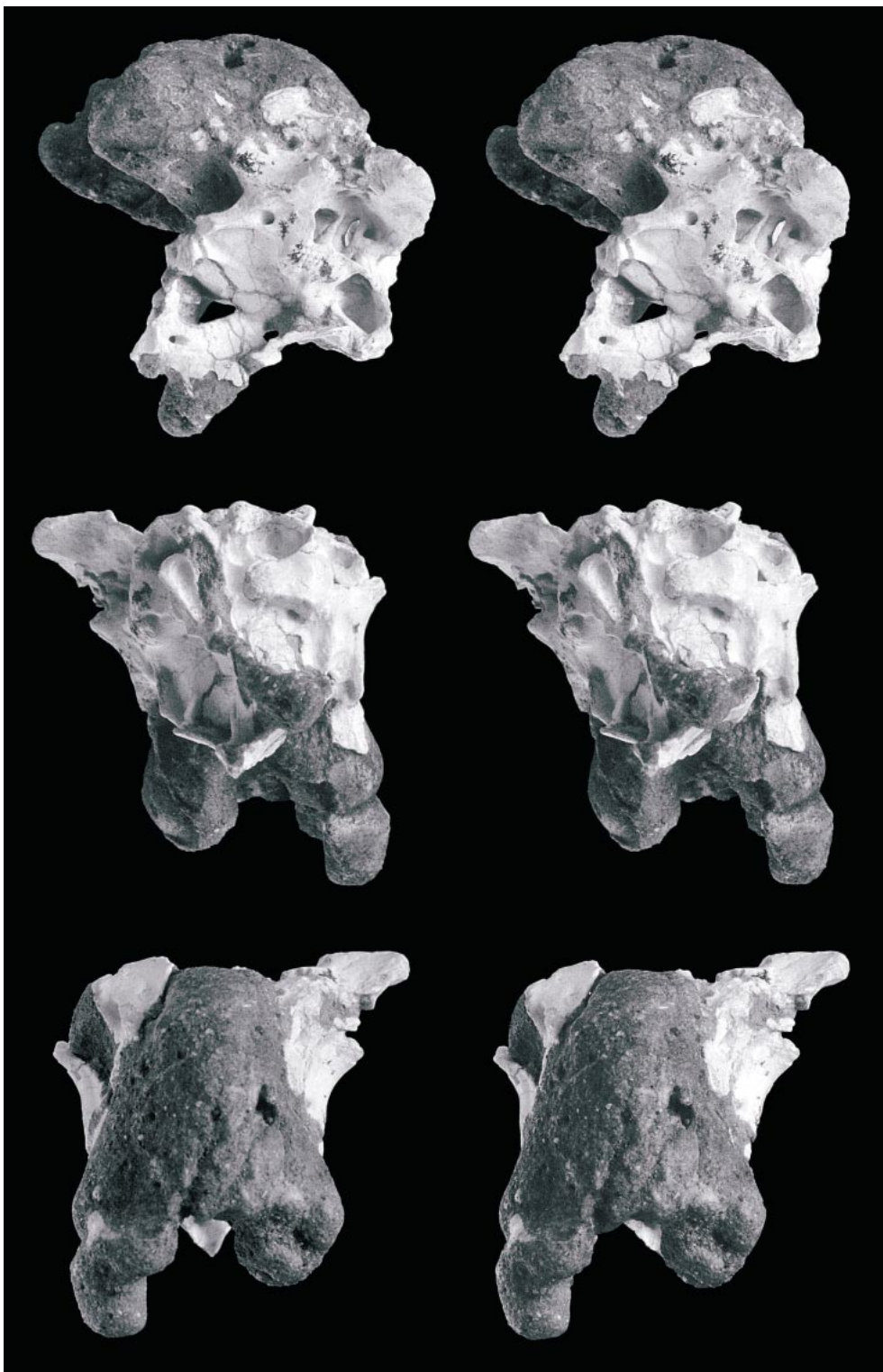


Fig. 15. The braincase of the holotype specimen IGM 100/983. Top, left lateral; middle, ventral; lower, dorsal views. Abbreviations are listed in Appendix 1.

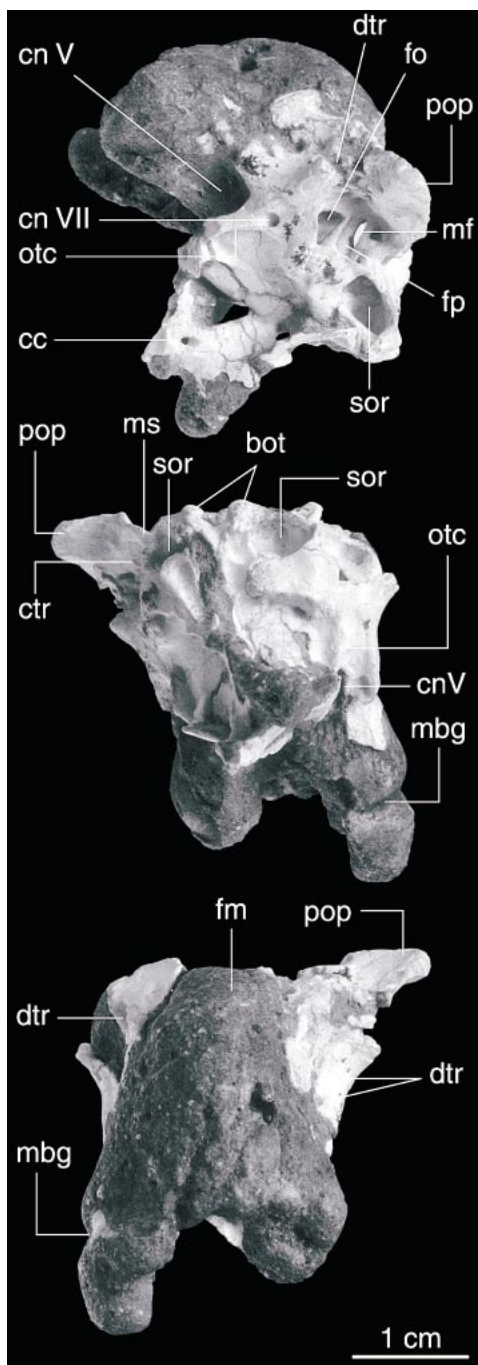


Fig. 15. Continued.

corresponds to the cochlear branch of CN VIII.

A minute foramen exits the anterior wall of the metotic foramen at mid-height. Its small size and proximity to the posterior part of the vestibular pyramid suggest that it is the opening of the perilymphatic duct (Makovicky and Norell, 1998). A similarly located foramen is present in ornithomimids (AMNH 5355) and *Velociraptor mongoliensis*. The posteromedial part of the inner ear is occupied by the metotic foramen. As in *Troodon formosus*, it is tall and narrow and displays an hourglass shape. The constriction of the metotic foramen is located slightly below mid-height. Asymmetry is present between the left and right ears in the region just posterolateral to the metotic foramen. On the right side, the single opening for the vagus and spinal accessory nerves and the dual foramina for the hypoglossal nerve open posterolateral to the posterior border of the metotic fissure (fig. 14). An additional foramen is present in this region on the left side of the skull (fig. 15). It opens laterally from the dorsal apex of the metotic foramen into the middle ear recess, thus opening anterior to the metotic strut and leading away from the occipital region of the skull. Another small foramen is present below the one just described, connecting the posteroventral corner of the middle ear to the subotic recess. Again, this feature is absent on the right side of the skull, although several small depressions in the roof of the subotic recess suggest that some resorption of bone has occurred in this region. Because it is only present on one side, this foramen is unlikely to represent the course of the stapedial artery.

A pair of foramina open into the base of the paroccipital processes from the roof of the lateral depression (fig. 15) and suggest that a posterior tympanic recess was present, albeit diminutive, unlike the condition described for *Troodon formosus* (Currie and Zhao, 1993). Given the abbreviated length of the paroccipital processes, this recess must have been relatively small in volume. A pit anterodorsal to the base of each paroccipital process is here interpreted as part of the dorsal tympanic recess. Two additional pits on the right side suggest that the dorsal tympanic recess may have occupied much of the

dorsolateral surface of the posterior region of the braincase, although its trace is smaller than in other coleurosaur. The left side is damaged in the region anterodorsal to the paroccipital process, so the presence of these pits cannot be verified.

CN VII exits the braincase laterally and slightly anteriorly through a deep, funnel-like channel situated at the posterodorsal terminus of the otosphenoidal crest (figs. 14, 15). Only the posterior rim of the opening of CN V is preserved on either side. In relative dimensions, *Byronosaurus jaffei* has a proportionately larger CN V opening than either *Troodon formosus* (Currie and Zhao, 1993) or *Saurornithoides junior*, although this is probably allometric. Both of these foramina are situated in a wide, shallow trough bordered by the otosphenoidal crest below and a horizontal ridge that borders a lateral expansion of the braincase above. The latter structure markedly overhangs the exit of CN V, and a small pocket opens dorsally into this overhang. Other surfaces of the trough are also scalloped, a feature often associated with the presence of pneumatic diverticula.

The braincase is wide just dorsal to the exits of CN V (fig. 15). Dorsal to this lateral expansion, each side of the braincase curves medially, and the lateral surface is concave both transversely and parasagittally. The dorsal sagittal region is not preserved, but this area would have been roofed over by the posterior recesses of the parietals anteriorly and supraoccipital posteriorly.

INTERIOR OF BRAINCASE AND ENDOCAST

Most of the roof and lateral walls of the braincase are missing, but a well-consolidated natural endocast of the braincase with a smooth surface is preserved (fig. 15). The region of the endocast representing the cerebellar region lies beneath the supraoccipital and above the foramen magnum. It is prominently domed both sagittally and transversely, and it indicates that the cerebellar region of the brain was proportionately as large as in *Troodon formosus* (Currie and Zhao, 1993). Beneath the cerebellar area, the floor of the braincase is deeply concave. The combination of this deeply concave floor and the large foramen magnum suggest a large pons

and medulla. Anterodorsal to the exit for CN V the laterosphenoids widen laterally to accommodate the tectal and optic lobes. The anterior border of the tectal lobes is demarcated by a deep, oblique groove, which is dorsal to the level of the hypophyseal fossa (figs. 14, 15). Rostral to this groove the right side of the endocast preserves the base of the cerebral hemisphere, but this structure is insufficiently preserved to deduce relative size compared with other cerebral structures.

The inner surface of the posterior region of the braincase has been prepared up to the level of the opening of CN VII. The vestibular pyramid bulges into the brain cavity opposite the anterodorsal corner of the base of the paroccipital process. The apex of the vestibular pyramid is directed anteromedially. Anteroventral to the apex of the pyramid, the auricular fossa containing the foramina for CN VII and the cochlear and vestibular branches of CN VIII extends laterally from the base of the cerebellar portion of the endocast. On both sides of the braincase, the bony wall of the braincase is shattered in the region of the floccular recess. Damage to the surface of both pyramids precludes identification of the opening of the endolymphatic duct. The vertical vestibular canal is not excessively swollen. The metotic foramen is situated posteroventral to the vestibular pyramid, while the exit of CN VII constrains the base of the vestibular pyramid anteriorly. The exit of CN VII is visible as a larger foramen located anterior to the vestibular pyramid, at approximately the same level as the opening for CN VIII.

SCLERAL OSSICLES: Articulated anterior segments of both scleral rings are preserved in the anterior part of the orbit on IGM 100/983, two ossicles on the right and three on the left (figs. 2, 3). Some of the remaining ossicles may lie in a mass of fragmentary bones just ventral to the orbit, but most of these fragments seem to be from the jugal and mandible. The five ossicles are incompletely exposed, but they are generally similar to those of troodontids (e.g., *Saurornithoides mongoliensis*) and other basal coleurosaur in being rectangular with only a gentle lateral convexity.

THE MANDIBLE

DENTARY: The dentaries are partly eroded, but from the preserved sections it can be determined that they are thin with slightly concave dorsal and convex ventral margins (figs. 2, 3). Like other troodontids they are tall posteriorly and taper anteriorly toward the symphysis. The lateral surface is scoured by a deep median groove filled with numerous small foramina, just below the tooth row. Posteriorly, this groove disappears as the lateral surface of the dentary becomes flat; a small ridge overhangs the lateral surface dorsally. CT scans show that the groove is level lying with the implanted bases of the tooth roots. Small perforating canals that pass between the roots of consecutive teeth connect the lateral canal and the Meckelian groove, transmitting branches of the mandibular nerve and artery. CT scans also show that the Meckelian groove parallels the lateral groove along the inner surface of the mandible. The groove terminates dorsal to a foramen

Similar to *Sinornithoides youngi* (Rusell and Dong, 1993) the dentaries are parallel in ventral view, and there is no medial curvature of the rami at the mandibular symphysis, as there is in *Saurornithoides mongoliensis*, *Saurornithoides junior*, and *Troodon formosus* (fig. 3).

SPLENIAL: Only fragments of the splenial are exposed, in ventral view. The anterior extent of the splenial is hard to determine; however, it reaches at least as far anteriorly as beneath the accessory antorbital fenestra (fig. 3). It is apparently longer than in *Deinonychus antirrhopus* and more similar to the condition in the dromaeosaurids *Velociraptor mongoliensis* and *Dromaeosaurus albertensis* where the splenial is at least half the length of the dentary. Posteriorly, the splenial wraps around the ventral surface of the dentary to become exposed laterally, beneath the anterior end of the antorbital fenestra. Whether the splenial is significantly exposed laterally as a triangular surface as in *Saurornithoides junior*, *Saurornithoides mongoliensis* (personal obs.), and dromaeosaurids (Currie, 1995) cannot be determined.

SURANGULAR: The surangular is only preserved as pieces on the right side of the skull,

and little morphology can be ascertained (fig. 2). It is transversely convex and apparently narrow dorsal to the mandibular fenestra, suggesting that the mandibular fenestra was large, unlike the condition in dromaeosaurids. Just ventral to the lacrimal buttress, a large, elliptical surangular foramen perforates the surangular; anterior to this foramen the bone is slightly concave, but lacks a distinct groove as in some other theropods (e.g., *Ornitholestes hermanni* and *Dromaeosaurus albertensis*).

ANGULAR: The right angular is also extremely fragmentary (fig. 2). The element is crescentic, with an expanded lateral surface anteriorly. More anteriorly the bone is fragmented.

DENTITION

The dentition of *Byronosaurus jaffei* is unusual for theropod dinosaurs in that no serrations are found on the anterior or posterior carinae (fig. 16), a feature known only in Alvarezsaurids, the ornithomimosaur *Pelecanimimus polyodon*, and toothed avialans. Four premaxillary teeth are present, but it is difficult to determine the number of maxillary or dentary teeth because these areas are poorly preserved. Nevertheless, the preserved teeth are densely packed, and a conservative estimate using the spacing of the preserved teeth to estimate the number of missing teeth is that at least 30 maxillary teeth and 30 dentary teeth were present.

All of the teeth are recurved with symmetrical carinae and somewhat bulbous crown bases (fig. 16). The tooth bases are marked by mediolateral, longitudinal grooves. The premaxillary teeth are small and closely packed, and they are round in cross section. The maxillary teeth are small compared with similar-sized theropods. They are also heterodont, with larger teeth occupying the 11th and 12th tooth positions. The more anterior teeth are round in cross section, grading into elliptical and then subrectangular teeth posteriorly.

POSTCRANIAL SKELETON

Limited postcranial remains were preserved with the holotype, including several vertebrae from the presacral part of the ver-

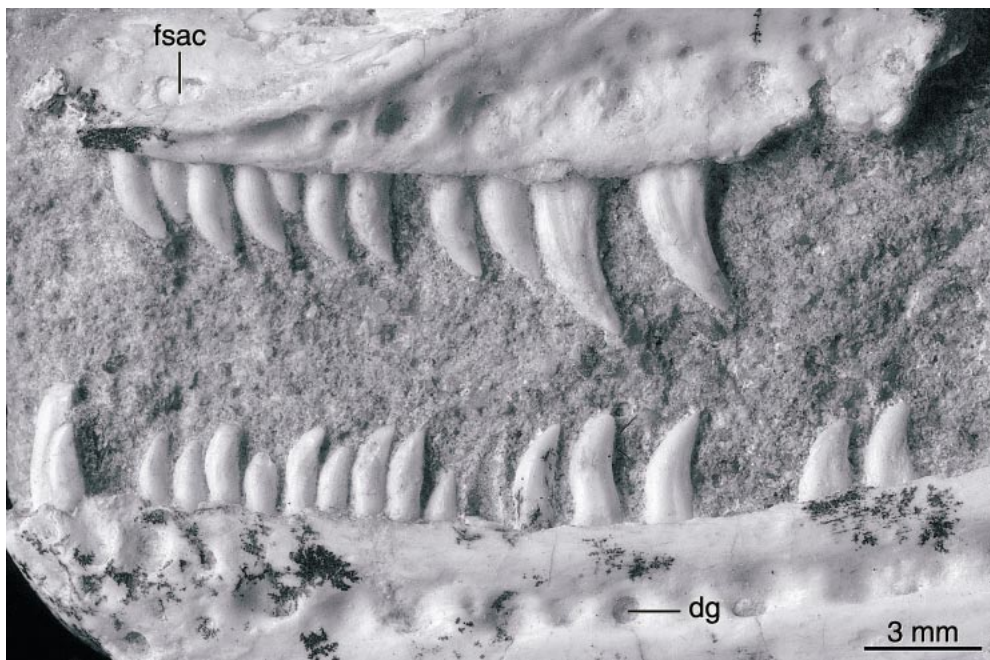


Fig. 16. The teeth of the right maxilla and dentary of the holotype (IGM 100/983). Notice both the lack of serrations and the heterodont condition.

tebral column and tail. Hindlimb elements include a heavily weathered element that represents the proximal end of the right femur, the right knee, a number of broken and weathered sections of hollow limb bones, and a number of pedal phalanges. None of the preserved vertebrae are complete.

The preserved cervical elements are identified as parts of the axis and third and fourth cervicals. Two nodules each contain parts of two articulated anterior cervicals. Only the posterior half of the neural arch and the posteriormost end of the centrum are preserved on the more anterior cervical. The postzygapophyses are set far from the midline and are surmounted by small epipophyses. The base of the neural spine is preserved and it appears to have been anteroposteriorly short along the midline. The following cervical is better preserved and comprises the majority of the centrum and the anterior half of the neural arch (fig. 17). The prezygapophyses diverge widely from the midline and face anterodorsally and slightly medially. Small, anterior pedicular fossae are present just lateral to the floor of the neural canal. Laterally, the

borders of the neural arch arc ventrally and overhang the centrum. The broken posterior end of the centrum reveals that the interior was hollow, and a small foramen on the side of the centrum probably marks the pneumatic connection to the interior. Nearly complete cervical ribs are preserved in articulation with both the centrum and arch of the second cervical in the nodule. The capitulum and tuberculum are axially elongate. A short, anterior process extends a short distance anterior to the juncture between the tuberculum and capitulum, and a small pneumatic foramen is visible on the medial face of the left rib in this region. Posterior to this juncture the main shaft of the cervical rib has a long, tapering, transversely flattened shaft.

A second, smaller nodule contains the anterior portion of the anterior vertebra from the nodule described above as well as the posterior part of the preceding element. This, the anteriormost preserved cervical, has a small but proportionately massive neural arch. The arch narrows rostrally, suggesting that it was triangular in dorsal view, as is characteristic of the theropod axis. The single

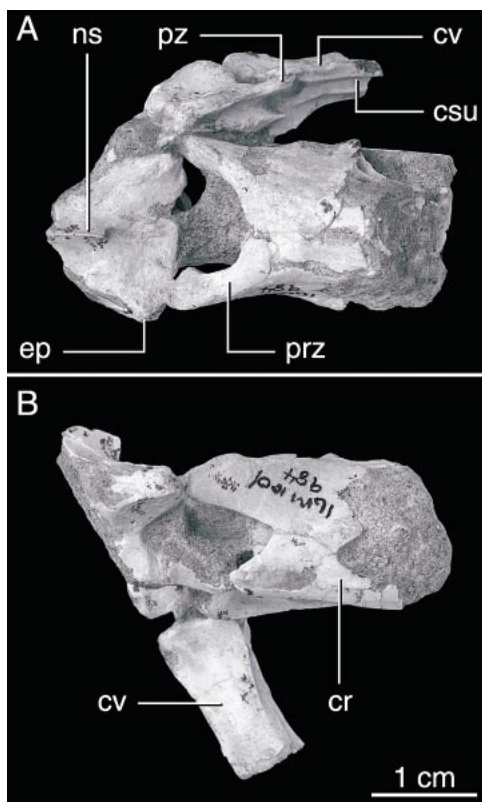


Fig. 17. Cervical and caudal vertebrae of IGM 100/984 in (A) posterodorsal and (B) dorsal views. Abbreviations are listed in appendix 1.

preserved postzygapophysis is surmounted by a massive, rugose epipophysis, suggesting that it derives from the axis (Gauthier, 1986). The following element is heavily abraded but displays a steeply angled anterior intercentral articulation typical of the anteriormost post-axial cervicals.

Four weathered sections of the dorsal series are preserved. One of these sections comprises two centra with a tall narrow cross section and large hypapophyses (fig. 18). The more anterior vertebra has the hypapophysis situated at the front end of the centrum, whereas this structure occupied a greater length on the second vertebra. These vertebrae clearly derive from the very front of the dorsal series. More posterior sections have more rounded centra and diminutive zygapophyseal facets that are situated close to the midline. The postzygapophyses arc ventrally

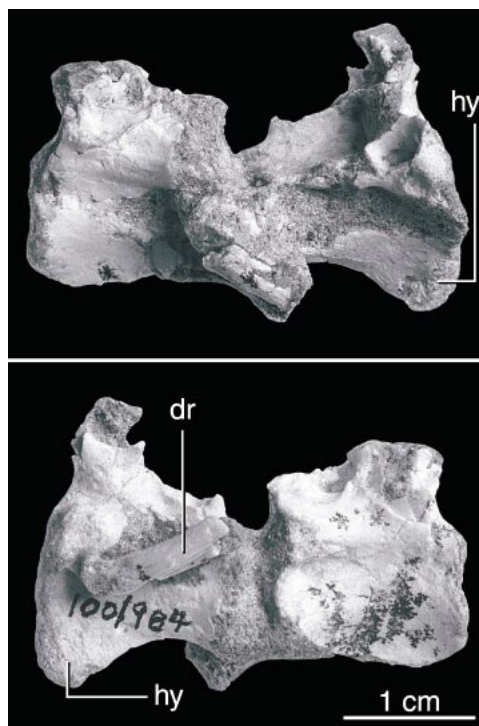


Fig. 18. Dorsal vertebrae of IGM 100/983 in right and left lateral views. Abbreviations are listed in appendix 1.

toward their medial borders, forming hypospheneal articular facets.

A single, apneumatic centrum, which is wider than tall, may derive from the sacrum, but this cannot be determined for certain. Four fragments of distal caudals are preserved, two of these are articulated and appressed to the larger piece containing anterior cervicals. The centra of the distal caudals are large and laterally constricted. The prezygapophyses are broken but do not appear to have been elongated as in basal tetanurines, because their preserved parts taper rapidly. The neural canal is diminutive, and a distinct sulcus extends above it along the roof of the neural arch. A similar sulcus is also present in other troodontids (Russell, 1969; Russell and Dong, 1993).

A right knee composed of the proximal ends of the tibia and fibula and the distal extremity of the femur is poorly preserved, and little morphology is apparent (fig. 19). The distal femur possesses a marked popliteal

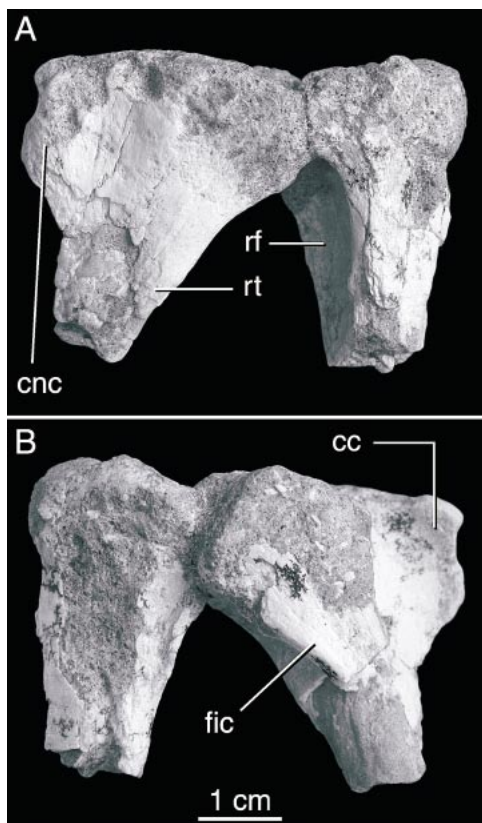


Fig. 19. Right knee of the holotype specimen IGM 100/983 in (A) medial and (B) lateral views. Abbreviations are listed in appendix 1.

fossa. The distal condyles are narrow and extend far posterior to the femoral shaft. A long, narrow supracondylar crest extends from the lateral condyle toward the proximal end of the femur.

The proximal end of the tibia is subtriangular in proximal view. Both the cnemial crest and the lateral condyle of the tibia are well developed and project far from the shaft. The cnemial crest is subtrapezoidal in medial view and curves laterally at its anterior rim. A large, suboval tuberosity marks the proximodorsal extremity of the cnemial crest, and the anterior border below it is thickened for muscular insertion. No details are evident on the short preserved section of the fibula. A number of hollow limb bone fragments pertain to the hindlimbs, but they do not warrant description.

The distal end of right metatarsal II is the

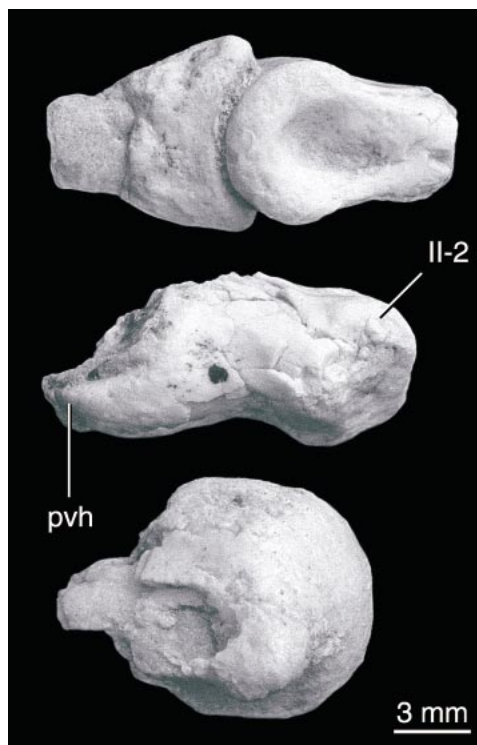


Fig. 20. Pedal phalanges of the holotype specimen IGM 100/983. Abbreviations are listed in appendix 1.

only part of the metatarsus preserved. The articulation is narrow and simple, with a more pronounced medial than lateral collateral ligament fossa. A pronounced, narrow ridge forms the posteromedial edge of the articulation but is broken a short distance above its distal terminus.

Fragments of three pedal phalanges were found with the holotype of *Byronosaurus jaffei* (fig. 20). One of these can be identified as the second phalanx of the second digit because of the presence of an elongated heel proximoventrally. As in other troodontids, but in contrast to derived dromaeosaurids like *Velociraptor mongoliensis* and *Deinonychus antirrhopus*, the pinched shaft between the articular ends is not foreshortened (Currie and Peng, 1993). The medial face is vertical, whereas the lateral one is convex, a feature that allows determination that the phalanx derives from the right foot. Erosion has destroyed much of the distal ginglymus. In profile, the phalanx resembles the corresponding

bone in *Troodon formosus* (Currie and Peng, 1993) and an indeterminate troodontid from Mongolia (Barsbold et al., 1987).

The other phalangeal fragments consist of articulated distal and proximal ends of two phalanges. Dorsodistally, the articulation of the proximal element bears a lappetlike extension of the articular surface. The articulated proximal end of one phalanx is triangular in cross section and the rest of the element appears to have been relatively slender. By comparison with *Borogovia gracilicrus* (Osmólska, 1987), these fragments may represent the phalanges III-2 and III-3.

DISCUSSION

Byronosaurus jaffei is one of the best preserved troodontid dinosaurs yet discovered and extends our knowledge on the diversity of Late Cretaceous troodontids. A number of important characters such as an extensive secondary palate, the opening here interpreted as a subnarial foramen, and the connection between the antorbital and accessory fenestrae though the interfenestral bar were previously unrecognized in troodontids. Unusually among troodontids, the teeth are unserrated. Prior to the discovery of *Byronosaurus jaffei* and *Sinovenator changii* (Xu et al., 2002), most known troodontid teeth were characterized by large, apically curved denticles with "blood pits" between them (Currie et al., 1990). The only exception is an unnamed troodontid from Mongolia, which apparently has reduced denticles that extend perpendicular to the axis of the tooth (Barsbold et al., 1987).

Byronosaurus jaffei provides us with the first data on the anatomy of the anterior part of the troodontid palate. The palate is formed anteriorly by the premaxilla and more posteriorly by the palatal shelves, which are flat anteriorly and become more vaulted posteriorly (figs. 4, 12). Premaxillary contribution to the roof of the palate is limited compared to other coelurosaurs. The vomers appear fused anteriorly and are divided posteriorly at the level of the interfenestral bar (fig. 12). The vomers apparently lay between the palatal shelves posteriorly and lie dorsal to them more anteriorly. They extend anterior to the

interfenestral bar; however, they apparently did not extend along the roof of the palate anteriorly beneath the nares as in *Velociraptor mongoliensis*.

An unusual feature of *Byronosaurus jaffei*, which is also present in the alvarezsaurid *Shuvuuia deserti*, is the presence of a small tubular foramen on the maxilla just dorsal to the tooth row on the ventral border of the narial fossa (fig. 6). We interpret this feature as homologous to the subnarial foramen, which typically lies in the premaxillary-maxillary suture and level with the supraalveolar canal in theropods and presumably transmitted parts of the maxillary branch of CN V that innervated the tip of the snout. This opening extends into a tubular sinus adjacent to the tooth row (the supra-alveolar canal [Norell et al., 2000]). A very similar configuration is seen in *Shuvuuia deserti* (IGM 100/977). If our interpretation of this feature is correct, then Sereno's (2001) assertion that alvarezsaurids lack a subnarial foramen needs to be modified.

The internarial bar in most theropod dinosaurs is an oval or cylindrical rodlike structure composed of the premaxillae that meet the nasals posteriorly. Sereno (2001: 93) asserted, in reference to his placement of alvarezsaurids as the sister group to ornithomimosaurs, that "the unusual dorsoventral flattening of the internarial bar ... is unique to these two groups." However, this configuration is also present in the troodontid taxa *Saurornithoides junior* and *Byronosaurus jaffei*.

The interfenestral bar in *Byronosaurus jaffei* shows some unique features (figs. 7–10). Unlike other troodontids, the interfenestral bar is not inset from the plane of the maxilla, but is flush with the lateral surface of the snout. As in both species of *Saurornithoides*, a connection between the antorbital and accessory antorbital fenestrae passes through the interfenestral bar (figs. 9, 10). The nasal passage terminates at the dorsal end of the interfenestral bars in *Byronosaurus jaffei*, and it opens into the choanae at the level of the antorbital fenestra (fig. 9). Our previous description (Norell et al., 2000) stated unclearly that the nasal passages are connected to the antorbital fenestra by a connection through the interfenestral bar, but an exposed

cross section of this region in the referred specimen clearly shows that it is the nasal passage proper that transits the interfenestral bar.

Although *Byronosaurus jaffei* shares derived dental characters related to tooth spacing and shape with other troodontids, it differs in having unserrated teeth (fig. 16). This has important implications toward understanding the phylogenetic position of troodontids. Some previous analyses have grouped the Troodontidae with therizinosaurs (and the edentulous oviraptorosaurs) in part because of the enlarged and apically hooked serrations seen in members of both groups. The presence of small serrations in the recently described basal troodontid *Sinovenator* (Xu et al., 2002) and the absence of serrations in *Byronosaurus jaffei* clearly show that large denticles can no longer be regarded as plesiomorphic within Troodontidae, and are diagnostic of a more exclusive clade within Troodontidae.

PHYLOGENY

In our preliminary description of *Byronosaurus jaffei* (Norell et al., 2000), we examined the relationship of *Byronosaurus jaffei* to other troodontids and found it to be the sister group to a clade of derived large-bodied troodontids comprising *Troodon formosus* and both species of *Saurornithoides*. More recent studies of coelurosaurian relationships (Norell et al., 2001; Xu et al., 2002) have included almost the same sampling of troodontid taxa as our preliminary study and have yielded results that are largely congruent with it.

Here we have expanded the Xu et al. (2002) study, which included the data of Norell et al. (2000), by adding an unnamed taxon from the Early Cretaceous of Mongolia (Barsbold, 1987) and several characters, some of which pertain to troodontid relationships. Seven troodontid species are included along with 42 other coelurosaurian taxa and the tetanuran *Allosaurus*, which was used to root the most parsimonious trees. The complete matrix has 220 characters and 50 taxa, and the character list and data matrix are available at <http://research.amnh.org/users/norell/index.html>. The troodontids *Borog-*

via gracilicrus and *Tochisaurus nemegtensis* were excluded, because apart from the autapomorphic phalangeal characters of the former, the single known specimen of each species only shows characters that are common to all troodontids more derived than *Sinovenator*, and thus provides no information toward elucidating troodontid relationships. Our comprehensive approach of analyzing troodontid relationships in the broader context of coelurosaurian phylogeny is justified by the lack of consensus regarding the relationship of Troodontidae to outgroup taxa. Furthermore, the high amounts of homoplasy and missing data that pervade coelurosaurian relationships complicate the correct establishment of character polarities. In our view, the least assumptive approach to this problem is to analyze a comprehensive range of outgroup taxa (i.e., Coelurosauria) to achieve an accurate optimization of ancestral states at the root node of Troodontidae.

All characters were treated as unordered. Analysis of this dataset was conducted using NONA version 1.9 (Goloboff, 1999) run through the Winclada interface (Nixon, 1999). One thousand repetitions of the tree bisection regrafting algorithm were used to find islands of shortest trees, followed by branch swapping to find all shortest trees. The analysis found 432 trees (TL = 586, CI = 0.45, RI = 0.75), and a strict consensus tree is presented in fig. 21. Troodontid taxa are boldfaced.

Troodontids are found to be monophyletic and are the sister taxon of the Dromaeosauridae within a monophyletic Deinonychosauria, which in turn is the sister taxon to Avialae. Troodontid monophyly is well supported by the nine characters discussed below.

Dentary nutrient foramina situated in a horizontal groove on labial face of dentary: The labial margin of the dentary is pierced by a disparate number of nutrient and nervous foramina in theropods. In *Byronosaurus jaffei* (figs. 2, 3), *Troodon formosus* (Russell, 1969), *Saurornithoides mongoliensis*, *Saurornithoides junior* (Barsbold, 1974), and *Sinovenator changii* (Xu et al., 2002) these foramina line the floor of a distinct sulcus on the labial side of the dentary (Currie, 1987). In *Sinovenator changii* this groove is restricted to the posterior part of the dentary

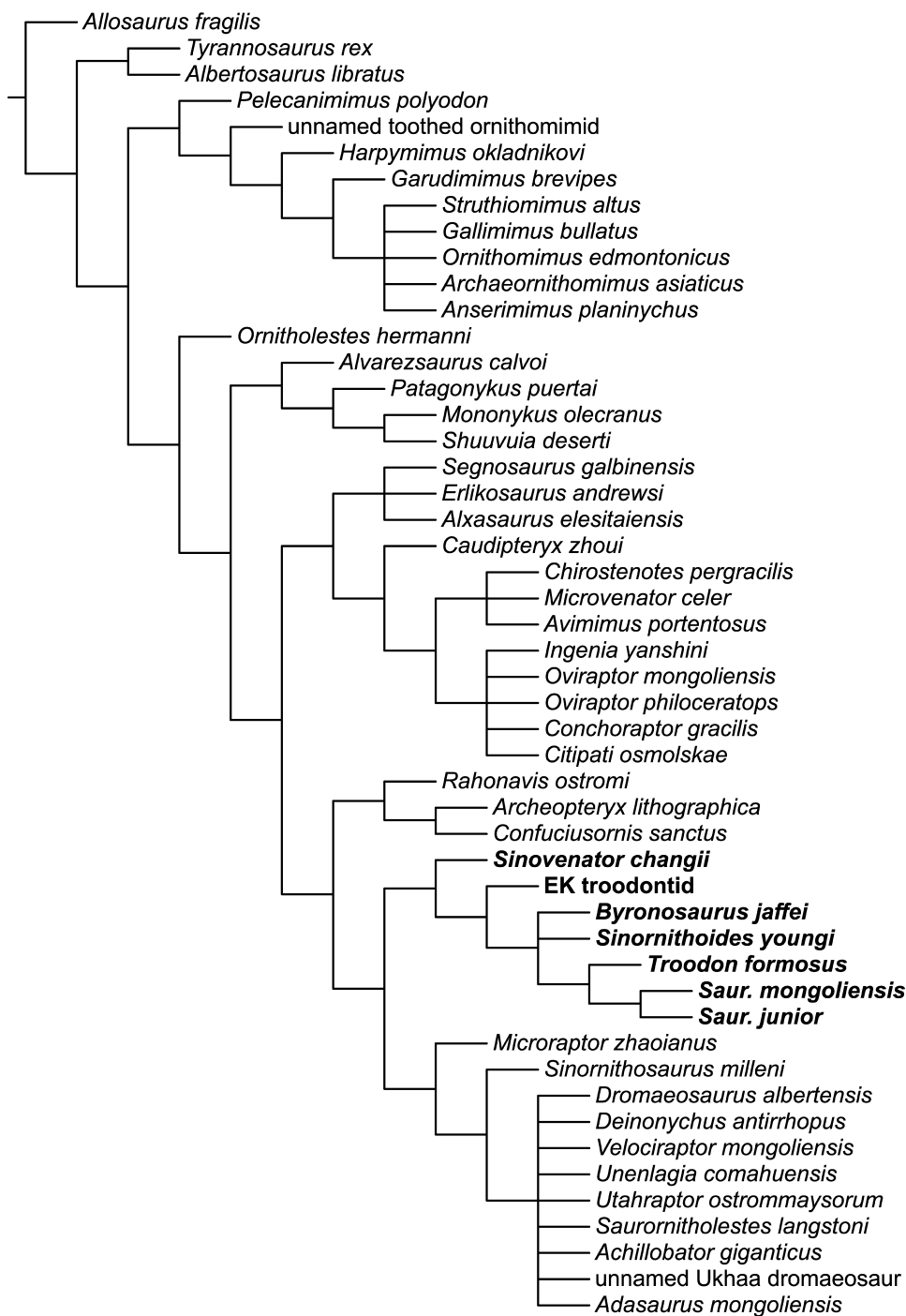


Fig. 21. Strict consensus of coelurosaurian interrelationships found in our phylogenetic analysis of 220 characters in 50 coelurosaurian taxa. Troodontids are indicated in bold.

ventral to the caudal end of the tooth row, but in more derived taxa it extends further toward, but does not reach, the symphysis. In dromaeosaurids, oviraptorids, and other maniraptorans the neurovascular foramina are linearly arranged but do not lie in a groove.

Pneumatic quadrate with pneumatopore on posterior face: The quadrate bears a pneumatic foramen posteriorly in the troodontid taxa where it is known, including *Troodon formosus* (Varrichio, 1997), an unnamed Early Cretaceous troodontid (Barsbold et al., 1987), and *Sinovenator changii* (Xu et al., 2002). Quadrate pneumaticity is variably expressed among coelurosaurian theropods. It is observed in tyrannosaurids, advanced oviraptorids (Maryanska and Osmólska, 1997), the compsognathid *Sinosauropteryx prima* (Currie and Dong, 2001b), derived avialans, and possibly some, but not all, ornithomimosaurids (Makovicky and Norell, 1998). Quadrate pneumaticity is absent in many maniraptorans, including basal oviraptorosaurs such as *Avimimus*, alvarezsaurids, therizinosauroids (Clark et al., 1994), and *Ornitholestes hermanni*. It also appears to be absent in *Archaeopteryx lithographica* (Witmer, 1990; Elzanowski and Wellnhofer, 1996) and *Confuciusornis sanctus* (Chiappe et al., 1999).

Basisphenoid recess absent: A blind pocket, derived from the median pharyngeal system, invades the basisphenoid ventrally in most theropods and forms a deep pneumatic recess on the basicranium (Witmer, 1997). This basisphenoid recess is widespread in coelurosaurs and is seen in ornithomimids (Osmólska et al., 1972), oviraptorids (Clark et al., 2002), and dromaeosaurids (e.g., *Dromaeosaurus albertensis* AMNH 5356). This recess is secondarily lost in troodontids (Currie, 1985), although the basisphenoid is hollow and pneumatic in at least *Troodon formosus*, *Byronosaurus jaffei* (fig. 15), and *Saurornithoides junior*. Secondary loss of the basisphenoid recess is also observed in the therizinosauroid *Erlikosaurus andrewsi* (Clark et al., 1994) and in advanced avialans. The condition is unknown for *Archaeopteryx lithographica* and *Confuciusornis sanctus*.

Dorsoventrally flattened internarial bar: As discussed above, the internarial bar

of troodontids appears to be dorsoventrally compressed (figs. 2, 5). Each premaxillary internarial process is wider than tall and has a dorsally flat surface, and the short nasal contribution to the narial bar forms a lateral extension of the base of the bar. This contrasts with the round internarial bar of dromaeosaurids such as *Velociraptor mongoliensis* (AMNH 6215) and uncrested oviraptorosaurs. A flattened internarial bar is derived independently in ornithomimosaurids and alvarezsaurids (Sereno, 1999). According to our analysis, this feature does not unambiguously optimize as a synapomorphy of any combination of these clades.

Closely packed anterior dentition in symphyseal region of dentary: The lower dentition of troodontids is moderately heterodont. In the dentary, the anteriormost teeth are closely packed, and toothless jaws show that the alveoli are confluent within a groove in the anterior part of the jaw (Currie, 1987). Posteriorly, the alveoli are separated by walls of porous interdental bone. In contrast, the teeth of most theropods are more equidistantly separated and set in separate alveoli throughout the whole jaw, as in dromaeosaurids (IGM 100/986, AMNH 5356) and *Archaeopteryx lithographica* (Elzanowski and Wellnhofer, 1996). The teeth of alvarezsaurids and the basal ornithomimosaur *Pelecanimimus* are set in a groove throughout the dentary, but are subequal in size. In therizinosauroids, all teeth are set in individual alveoli separated by septa, and the teeth grade toward larger size rostrally (Clark et al., 1994; Xu et al., 2001).

Depression on the ventral surface of the postorbital process of the laterosphenoid: A ventral pit is visible on the postorbital process of the laterosphenoid in *Troodon formosus* (Currie, 1985), *Saurornithoides junior* (IGM 100/1), and *Sinovenator changii* (Xu et al., 2002). The pit has smooth walls, and may have been pneumatic. The postorbital process of dromaeosaurids (AMNH 5356, PIN 100/25), *Archaeopteryx* (Walker, 1985; London specimen), oviraptorosaurs, therizinosauroids (Clark et al., 1994), alvarezsaurids, and ornithomimosaurids does not bear such a pit.

Reduced basal tubera that lie directly ventral to the occipital condyle: The basal

tubera are unusual among coelurosaurs in being reduced and situated close to the midline, so that they are directly ventral to the occipital condyle in Asian troodontid taxa (fig. 14). The tubera are separated by a narrow V-shaped notch in all troodontids. The tubera are larger in *Troodon formosus*, but they are still positioned close to the midline (Russell, 1969) and ventral to the condyle. In many outgroup taxa, including dromaeosaurids, oviraptorosaurs, and ornithomimosaurs, the tubera are more pronounced and lie in a parasagittal plane lateral to the occipital condyle. Alvarezsaurids have reduced tubera, but these are widely separated from each other by a notch that is wider than the diameter of the occipital condyle. The basal tubera of the therizinosauroid *Erlikosaurus andrewsi* are virtually obliterated by the ventral expansion of the pneumatic basisphenoid (Clark et al., 1994).

Large number of teeth: Among advanced theropods, troodontids are characterized by having a very large number of teeth (fig. 2). Although the precise number is unknown in *Byronosaurus jaffei*, a minimum of 4 premaxillary and 30 maxillary teeth were present in the upper jaws, while the dentary held 30 or more teeth. In dromaeosaurids the tooth count is substantially smaller—4 premaxillary, and 9 (*Dromaeosaurus albertensis*) to 15 (*Deinonychus antirrhopus*) maxillary teeth and 11 (*Dromaeosaurus albertensis*) to 16 (*Deinonychus antirrhopus*) dentary teeth (Ostrom, 1969, Currie, 1995). *Archaeopteryx lithographica* has a dental formula of 4 premaxillary plus 8 maxillary and 11 dentary teeth (Wellnhofer, 1974). Oviraptorosaurs and advanced ornithomimids are edentulous, but the basal ornithomimid *Pelecainimus polyodon* (Perez-Moreno et al., 1994) has more than 220 teeth in its jaws, and a large number of teeth are also present in the alvarezsaurid *Shuuuuaia* and in therizinosauroids. According to our analysis, these taxa derive the large number of teeth independent of troodontids.

Long, slender transverse processes: The transverse processes of the trunk vertebrae are relatively long and slender and curve slightly in troodontid taxa that preserve them, including *Sinoventor changii* and *Troodon formosus*. The transverse processes

are relatively short in dromaeosaurids such as *Sinornithosaurus millenii* (Xu et al., 1999) and *Velociraptor mongoliensis* (IGM 100/986) and in the basal avialans *Archaeopteryx lithographica* (Berlin specimen) and *Rahonavis ostromi* (Forster et al., 1998). Oviraptorosaurs have short, wide transverse processes on the trunk vertebrae (Makovicky and Sues, 1998). Proportionately long transverse processes are seen in ornithomimids and in alvarezsaurids.

In all troodontids for which the tail is known, the distal caudals have a sulcus on the dorsal midline in place of a neural spine, but the condition is unknown for the most basal troodontid *Sinovenator* and is thus an ambiguous synapomorphy of the clade. Several characters used to diagnose Troodontidae in the past no longer optimize at the base of Troodontidae, following the discovery of a number of new deinonychosaurs in recent years. The troodontid metatarsus is asymmetrical with a slender metatarsal II that is markedly shorter than metatarsals III and IV, and a robust metatarsal IV, unlike the more symmetrical metapodium of most other theropods, and this asymmetry has been used to diagnose the clade in the past (Wilson and Currie, 1985). Somewhat asymmetric metapodia are also observed in the basal dromaeosaurids *Microraptor zhaoianus* (Xu et al., 2000) and, to a lesser degree, in *Sinornithosaurus millenii* (Xu et al., 1999), and this character may be diagnostic of Deinonychosauria rather than of Troodontidae.

Possession of large, apically hooked denticles has also been considered a diagnostic character of troodontids (Barsbold, 1974; Currie, 1987). The recently discovered *Sinovenator changii* has small denticles directed perpendicular to the long axis of the tooth, however, and this character now diagnoses a more exclusive clade within Troodontidae. An inflated bulla at the base of the cultriform process has been observed in *Saurornithoides junior* and *Troodon formosus*, and it was previously viewed as a troodontid synapomorphy. It is, however, absent in the basal troodontid *Sinovenator changii* and its presence cannot be ascertained in several other taxa including *Byronosaurus jaffei*.

Within troodontids, *Sinovenator changii* is the sister taxon to a clade comprising all oth-

er troodontids. Two unambiguous synapomorphies are present at this node.

Presence of a subotic recess on the side of the braincase ventral to the middle ear:

A pneumatic pocket invades the lateral wall of the basicranium ventral to the middle ear in *Troodon formosus*, *Saurornithoides junior*, *Byronosaurus jaffei* (figs. 14, 15), and the Early Cretaceous troodontid from Khmareen Us (Barsbold et al., 1987). Witmer (1997b) termed this feature the subotic recess. A subotic recess is absent in dromaeosaurids, basal avialans, alvarezsaurids, and oviraptorosaurs. It is convergently present in at least some derived ornithomimosaurian taxa (Makovicky and Norell, 1998).

Metatarsal IV oval in cross section, deeper than wide: Basal paravians have a mediolaterally expanded metatarsal IV with a lateral flange on the side. This condition is seen in *Archaeopteryx lithographica* and *Rahonavis ostromi* and in dromaeosaurids, including *Microraptor zhaoianus* and *Velociraptor mongoliensis*. In higher troodontids, the fourth metatarsal reverses to a more columnar shape with an oval cross section that is longer along the palmar-plantar axis.

Byronosaurus jaffei and *Sinornithoides youngi* form a clade together with the larger bodied, Late Cretaceous *Troodon formosus*, *Saurornithoides mongoliensis*, and *Saurornithoides junior*. Two cranial characters unambiguously diagnose this group.

Large otosphenoidal crest defining lateral depression on side of braincase: Troodontids, with the exceptions of an unnamed Early Cretaceous form (Barsbold et al., 1987) and *Sinovenator changii*, bear a well-developed "lateral depression" (Barsbold, 1974) on the side of the braincase covering parts of the laterosphenoid, basisphenoid, prootic, and possibly part of the opisthotic. This lateral depression is delimited anteriorly and dorsally by the expanded otosphenoidal crest, which is formed by the laterosphenoid anteriorly and by the prootic and possibly also the opisthotic posteriorly. A number of small laminae subdivide the lateral depression into subcompartments, such as the prootic recess rostrally. The internal carotids enter the hypophyseal fossa near the rostral part of the lateral depression. The middle ear lies within the lateral depression in *Saurorni-*

thoides junior, but is dorsal to it in *Byronosaurus jaffei* (figs. 14, 15).

Presence of enlarged, distally oriented denticles: Theropod teeth are primitively serrated. In velociraptorine dromaeosaurids there are 5–7 denticles per millimeter (Currie et al., 1990), while this ratio is 3–3.2 denticles per millimeter in *Dromaeosaurus albertensis* (Currie, 1996). By contrast the number of denticles is 2.3–3 in *Saurornithoides mongoliensis* (Russell, 1969) and less than 2 per mm in *Troodon formosus* (Currie et al., 1990) and *Saurornithoides junior* (Barsbold, 1974). In addition, the denticles of these troodontid taxa are long and separated by deep blood grooves with small proximal blood pits. The teeth of *Sinornithoides youngi* have proportionately smaller serrations than do those of the three larger taxa listed above, but they are still proportionately large relative to tooth size (Currie and Dong, 2001a).

Relationships between *Byronosaurus jaffei*, *Sinornithoides youngi*, and a clade comprising the three larger bodied taxa *Troodon formosus* and both species of *Saurornithoides* cannot be parsed out, partly because the braincase is undescribed for *Sinornithoides* and the dentition is autapomorphic in *Byronosaurus jaffei*. The *Troodon* + *Saurornithoides* clade is derived in its possession of a medially deflected symphysis on the dentary and by the secondary loss of a dorsal tympanic recess.

ACKNOWLEDGMENTS

We thank the field crews of the 1993, 1994, and 1996 field seasons. For help in Mongolia, we would especially thank D. Baatar, T. Boldsukh, D. Dashzeveg, and R. Barsbold. Mike Novacek found the type specimen (IGM 100/983). Martin Kundrát carefully went over the manuscript. Amy Davidson and Bill Amaral prepared the specimens and Mick Ellison developed the figures. This work was supported by the Division of Paleontology at the American Museum, the Field Museum Department of Geology, and the Jaffe Family Foundation.

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APPENDIX 1

ANATOMICAL ABBREVIATIONS

II-2	pedal phalanx II-2	lpmx	left premaxilla
aof	antorbital fenestra	ls	left splenial
atr	anterior tympanic recess	mbg	groove separating forebrain and mid-brain of endocast
boc	base of occipital condyle	mf	metotic foramen
bot	basioccipital tuber	mg	mandibular groove
cc	common carotid foramen	ms	metotic strut
cf	carotid foramen	mx	maxillary fossa
cif	interfenestral crest	nar	naris
cnc	cnemial crest	nc	nasal chamber
cnV	cranial nerve v	ns	neural spine
cnVI	foramen for cranial nerve VI	otc	otosphenoidal crest
cnVII	foramen for cranial nerve VII	pn	pneumatic space
cn X,XI	foramen for cranial nerves X and XI	pop	paroccipital process
cnXII	foramen for cranial nerve XII	prz	prezygapophysis
csu	caudal vertebral sulcus	ps	palatal shelf
ctr	caudal tympanic recess	pvh	posteroventral heel
dg	dentary groove	pz	postzygapophysis
dr	dorsal rib	r	reconstructed
dtr	dorsal tympanic recess	ra	right angular
en	entrance to nasal chamber	rd	right dentary
ep	epipophysis	rf	right fibula
fic	fibular crest	rj	right jugal
fm	foramen magnum	rl	right lacrimal
fnc	floor of nasal chamber	rmx	right maxilla
fo	foramen ovale	rn	right nasal
fp	foramen pseudorotunda	rpmx	right premaxilla
fsac	foramen for supraalveolar canal (= subnarial foramen)	rs	right splenial
hf	hypophysial fossa	rsa	right surangular
hy	hypapophysis	rt	right tibia
iac	interantorbital canal	sac	supraalveolar canal
in	internarial bar	sf	surangular foramen
ifb	interfenestral bar	sor	subotic recess
ld	left dentary	t	tooth
ll	left lacrimal	v	vomer
lmx	left maxilla	waof	wall of antorbital fossa
ln	left nasal		

APPENDIX 2
MEASUREMENTS OF THE HOLOTYPE SPECIMEN IGM
100/983 (in mm)

Length from preserved caudal end of mandible to tip of rostrum	134.0
Length of upper tooth row (left)	79.0
Length of upper tooth row (right)	81.0
Length of dentary tooth row (right)	~66.0
Length of antorbital fenestra	38.0
Length of nares	~23.0
Length of maxillary fenestra	21.0
Max. transverse diameter of foramen magnum	7.5
Width across basal tubera	6.0
Length of left paroccipital process (from edge of foramen magnum)	13.0
Right tibial width (including cnemial crest)	33.0
Right distal cnemial crest dorsoventral length	13.0
Pedal phalanx II-2	16.0
